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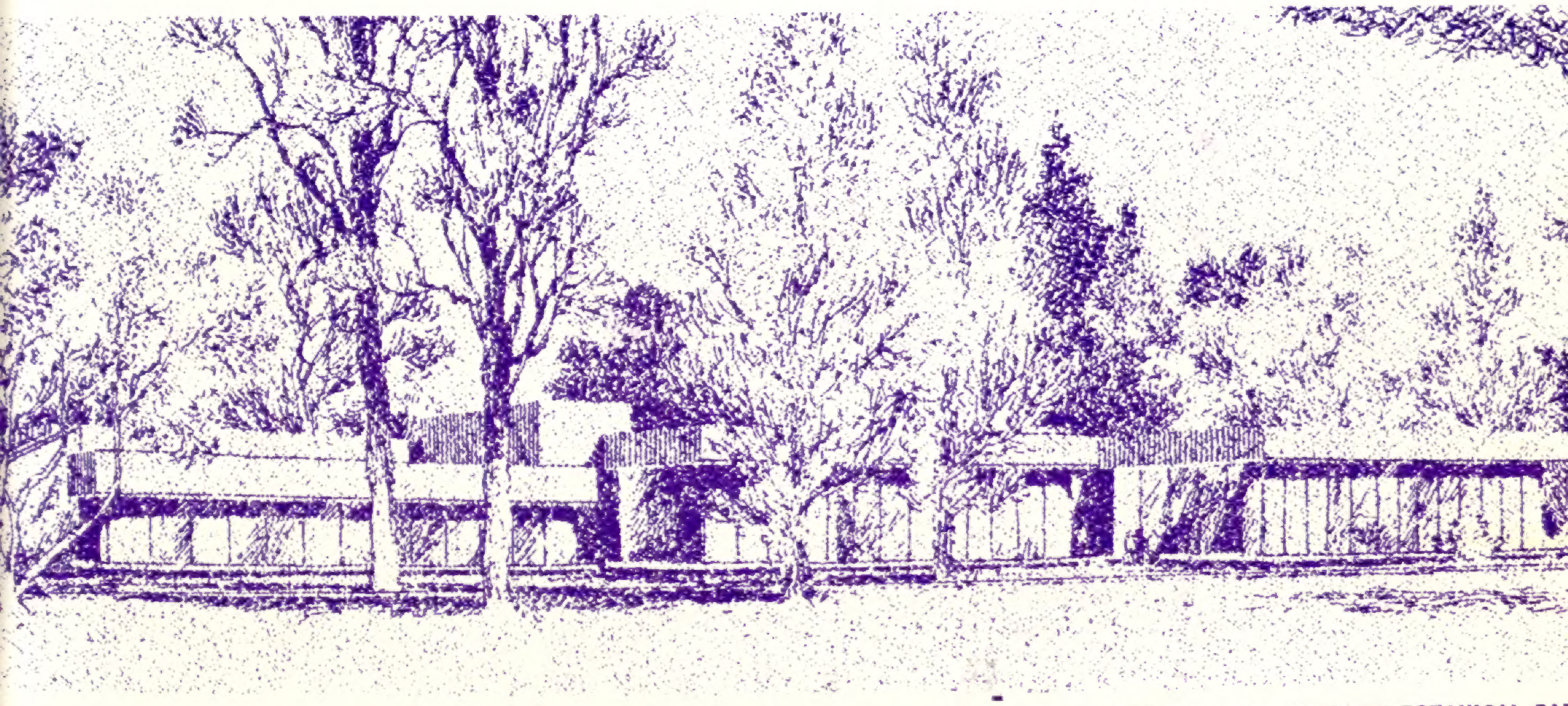

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EVOLUTION AND SYSTEMATICS OF THE GRAMINEAE: THE TWENTY-SIXTH SYSTEMATICS SYMPOSIUM

RICHARD W. POHL[1]

The Twenty-sixth Systematics Symposium was held at the Missouri Botanical Garden 19–20 October 1979 with partial support from National Science Foundation Grant DEB78-10180. Speakers at the Symposium were W. D. Clayton, Kew; H. E. Connor, Christchurch; Thomas R. Soderstrom, Washington, D.C.; G. Ledyard Stebbins, Davis; J. M. J. deWet, Urbana. Their contributions are published here. Other speakers, whose papers are not published in this issue, were Hugh H. Iltis, University of Wisconsin, Madison: "From Teosinte to Maize—The Incredible Transformation," Frank W. Gould,[2] Texas A&M University, College Station: "Evolution in the Genus *Bouteloua* Lag," and G. Davidse, Missouri Botanical Garden: "A Review of Chromosome Numbers in the Gramineae."

This was the first time in the Symposium's history that a specific plant family was chosen as a topic. The unrivaled economic importance of the grasses and their prominence in all major phytogeographic regions of the world seemed to be adequate reasons for this choice. The purpose of the Symposium was to review and reinterpret selected topics dealing with the evolution and systematics of the Gramineae.

In the western world, the history of the classification of the grasses began with the treatment of the group by Theophrastus (fourth century B.C.). In the first book in his *Enquiry Into Plants* (Hort, 1916), Theophrastus divided all plants into four groups: trees, shrubs, undershrubs, and herbs. Book VII of his treatment was entitled "Of Herbaceous Plants: Cereals, Pulses, and Summer Crops." Included in this chapter were wheat, barley, one-seeded wheat, rice-wheat, millet, and Italian millet. *Sesamum indicum* of the Pedaliaceae was included. This treatment was obviously utilitarian, and does not define the family as a distinct and inclusive unit.

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[1] Department of Botany, Iowa State University, Ames, Iowa 50011.

[2] Deceased 11 March 1981. See second article of this issue.

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The Herbalists generally utilized the major divisions of the Theophrastian classification. There was a tendency to group together the grasslike herbs—Juncaceae, Gramineae, and Cyperaceae—but none of the Herbalist authors erected a category which includes only grasses. Such oddities as *Ustilago, Ricinus, Triglochin, Sparganium, Typha,* and *Equisetum* were added from time to time. Tournefort (1700), in the early eighteenth century, listed many common grass genera, but included such interlopers as *Ricinus*. Jussieu (1789) was the first to apply the name Gramineae to the grasses, and to erect a group that included only grasses. His system of classification included 13 unnamed groups, based primarily on the number of stamens, styles, and florets in the spikelets. In 1833, Kunth described 13 tribes of grasses, many of them still in current usage. His treatment was followed essentially by Endlicher (1836–1840) and Steudel (1855). Bentham & Hooker (1883) published a classification for the Gramineae, dividing the family into two series, the Paniceae and Poaceae, both originally described by Robert Brown (1814). These series corresponded more or less to the two subfamilies, Panicoideae and Festucoideae, later utilized by Hitchcock.

Hackel (1887), in *Die natürlichen Pflanzenfamilien,* utilized an identical system, dividing the two series on the basis of the point of disarticulation. The most prevalent system of classification, especially in the Western Hemisphere, during much of the twentieth century is that of Alfred Spear Hitchcock. The Hitchcock system is roughly the same as that of Bentham and Hooker, but in the reverse order. The two large subfamilies given by Hitchcock are of very different phyletic merit. The Panicoideae, with a very few deletions, is a good natural unit, with great internal consistency in a plethora of characters. The Festucoideae of Hitchcock, on the other hand, was a virtual morass of convergent elements, which could not be resolved by use of the traditional characteristics of the inflorescence and spikelet. It was the task of twentieth century agrostology to restudy this group and to segregate its numerous divergent elements. Early work on the cytology of the grasses by Avdulov (1931) and the anatomy of leaf epidermis and cross-section by Prat (1932) indicated strongly that the subfamily Festucoideae should be dismembered and its disparate elements reassigned to more coherent units. These early publications stimulated a multitude of studies on many aspects of grass anatomy, cytology, and physiology which have greatly clarified our understanding of the phylogeny of the family. As a result of the new interest in grass classification, a symposium on The Natural Classification of the Gramineae was convened at the Ninth International Botanical Congress at Montreal in 1959. We are now, incidentally, celebrating the twentieth anniversary of that epochmaking event. In this symposium, discussions of the grass embryo by John Reeder, the leaf epidermis by Henri Prat, of polyploidy by Frank W. Gould, of leaf internal anatomy by W. V. Brown, of the reaction of seedlings to herbicides by Al-Aish, of grass serology by Fairbrothers and Johnson, and of general morphology by C. E. Hubbard, and others, were heard. A final summation by G. Ledyard Stebbins, Jr. suggested a new classification for the Gramineae (Stebbins & Crampton, 1961), resulting in a near total dismemberment of the subfamily Festucoideae. The new classification, which has since undergone minor modifications, was a monumental synthesis of diverse data from many fields of investigation. Current classifications usually list six subfamilies, mostly based upon

anatomical, cytological, and physiological bases, rather than the traditional inflorescence and spikelet characters. The new systems have greatly enhanced internal coherence and predictive value. However, the subfamilies and tribes so established may not be the most convenient for routine identification of specimens, and for this purpose, conventional artificial keys need to be designed and employed. There are many occasions, however, when simple anatomical investigations, quickly performed on fresh or dried material with the aid of a razor blade, will immediately reveal the proper assignment of an unknown with greater certainty than inflorescence or spikelet characters.

All systems of classification for the Gramineae, be they conventional or modern and synthetic, rely on characteristics of extant grasses, and in that sense, we are still faced with the "abominable mystery" of the origins of the Gramineae. The recent investigations of the surface anatomy of fossil grass anthoecia by Thomasson (1979), indicate that we can now trace the phyletic lines of at least some grasses (the stipoids) back to Miocene ancestors and forecast the introduction of the fourth dimension of time into our understanding of the grass family.

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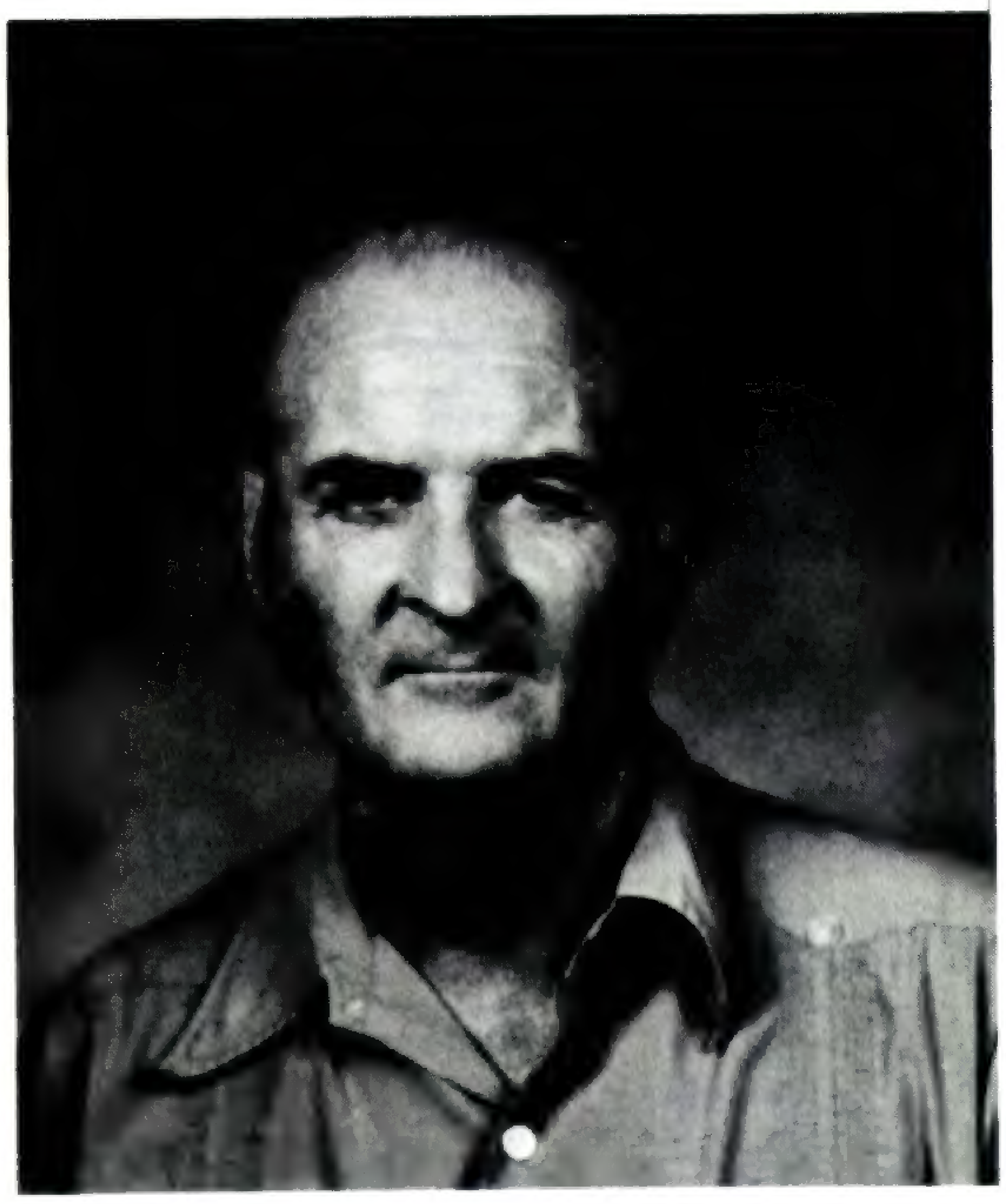
FRANK WALTON GOULD, 1913–1981

One of the leading agrostologists in the world and a speaker at the Twenty-sixth Systematics Symposium, Frank Walton Gould, died on 11 March 1981 after an illness with brain cancer. It seems most appropriate to include a short biographical sketch in his memory with this Symposium. His widow, Lucile Gould, has kindly provided the biographical information.—Editor.



Frank Walton Gould was born in Mayville, North Dakota, 25 July 1913, son of a geographer, with a brother and sister 2 and 4 years older. His third-grade year was spent at his father's hometown, Sheridan, New York, while his father completed work for his Master's Degree at the University of Michigan. From that time until he completed college, he lived where his father was eventually head of the geography department at what is now Northern Illinois University, Frank's alma mater. He missed celebrating the 50th anniversary of his DeKalb Township High School graduation by 2 months.

In 1935–1936 he completed work for his Master's Degree in Botany at the University of Wisconsin under Dr. Norman C. Fassett, surveying the prairie remnants of Dane County. In 1941 he completed his Ph.D. at the University of California at Berkeley under Dr. Lincoln Constance, monographing the liliaceous genus *Camassia*. During his graduate assistant work there with Dr. G. Ledyard Stebbins he became intrigued with the study of grasses—*Elymus*, etc. Also there he married his 40-year partner, Lucile. His first professorship was filling a year's vacancy at St. George, Utah; then 2 years at Compton Junior College, California. In southern California he continued his taxonomic studies of grasses with the aid of Dr. Carl Epling at U.C.L.A. In 1944 he became curator of the herbarium at the University of Arizona in Tucson. After 5 years he, his wife, and 3 daughters moved to College Station where he curated the Tracy Herbarium at Texas A&M University for 31 years, retiring as distinguished professor emeritus in 1979. However, a few years before his "retirement" he determined to pursue publication of a manual of the grasses of Mexico. He had much of the research done and had a good start on the manuscript at the time of his death.

In addition to some 80 publications, he authored 4 grass manuals: Southwestern USA, Texas Coastal Bend, Texas, Baja California (in press), and the well-known textbook, *Grass Systematics* (now being revised).—Lucile Gould.

EVOLUTION AND DISTRIBUTION OF GRASSES

W. D. Clayton[1]

Abstract

Recent developments in grass taxonomy give a new insight into their classification, and point to a phylogenetic sequence which maps differences in their internal metabolism. Corroboratory fossil evidence is unfortunately exceedingly meager, but it can be supplemented by examining the implications of present-day distributions. The subfamilies are distributed in worldwide climatic belts, but two-thirds of the genera are confined to single continents. Obviously, the genera are poor travellers, so how did the grasses become so widespread? Much depends on the probability of transoceanic transport. The evidence is inconclusive, but it seems likely that the tropical subfamilies spread during the first half of the Tertiary when the maximum water gap was 1200 km. Species distributions are likewise influenced by climatic differentiation and continental isolation. But they sometimes reveal the intervention of other factors, particularly the disruptive effect of climatic change in the Pleistocene. Data from the Afro-montane flora do not support the proposition that species from adjacent, but contrasting, ecological environments are distributed independently. Nor does a mapping of endemics encourage the concept of discrete centers.

Classification

Fundamental to most biological disciplines is the need to identify the organisms they work with, and the primary purpose of taxonomy is to satisfy this need by devising a standardized nomenclature, differential diagnoses and techniques for identification. One of the powerful concepts it has developed for achieving these aims is that of hierarchical classification.

In grasses this classification has traditionally been based upon similarities in spikelet structure. This provides an eminently practical system, but suffers from the defect that spikelets are subject to a good deal of parallel evolution. Yet the method should not be despised, for 80 years ago Stapf (1897) appreciated, on morphological grounds alone, that the Poeae and Eragrostideae were not particularly closely related. Nevertheless, even when parallel evolution was recognized, there was no criterion by which the true kinship could be determined.

The first revolution in classification occurred in the 1930s, when the taxonomic significance of leaf anatomy began to be appreciated. There was shown to be a major division between temperate and tropical tribes, and several subdivisions among the latter. With these findings it was possible to resolve many of the problems posed by parallel evolution, and to propose modifications with some confidence that the system was approaching closer to an expression of natural relationships.

The second revolution started in the 1960s, when it was shown that differences in leaf anatomy could be correlated with differences in photosynthetic pathway. It is now becoming clear that, at the higher levels, our classification maps variations in the internal metabolism of the plants.

Taxonomy, which set out to devise a practical filing system for cataloging plants, has thus acquired a classification which constitutes a source of biological evidence in its own right. To unravel its meaning is inevitably speculative, but

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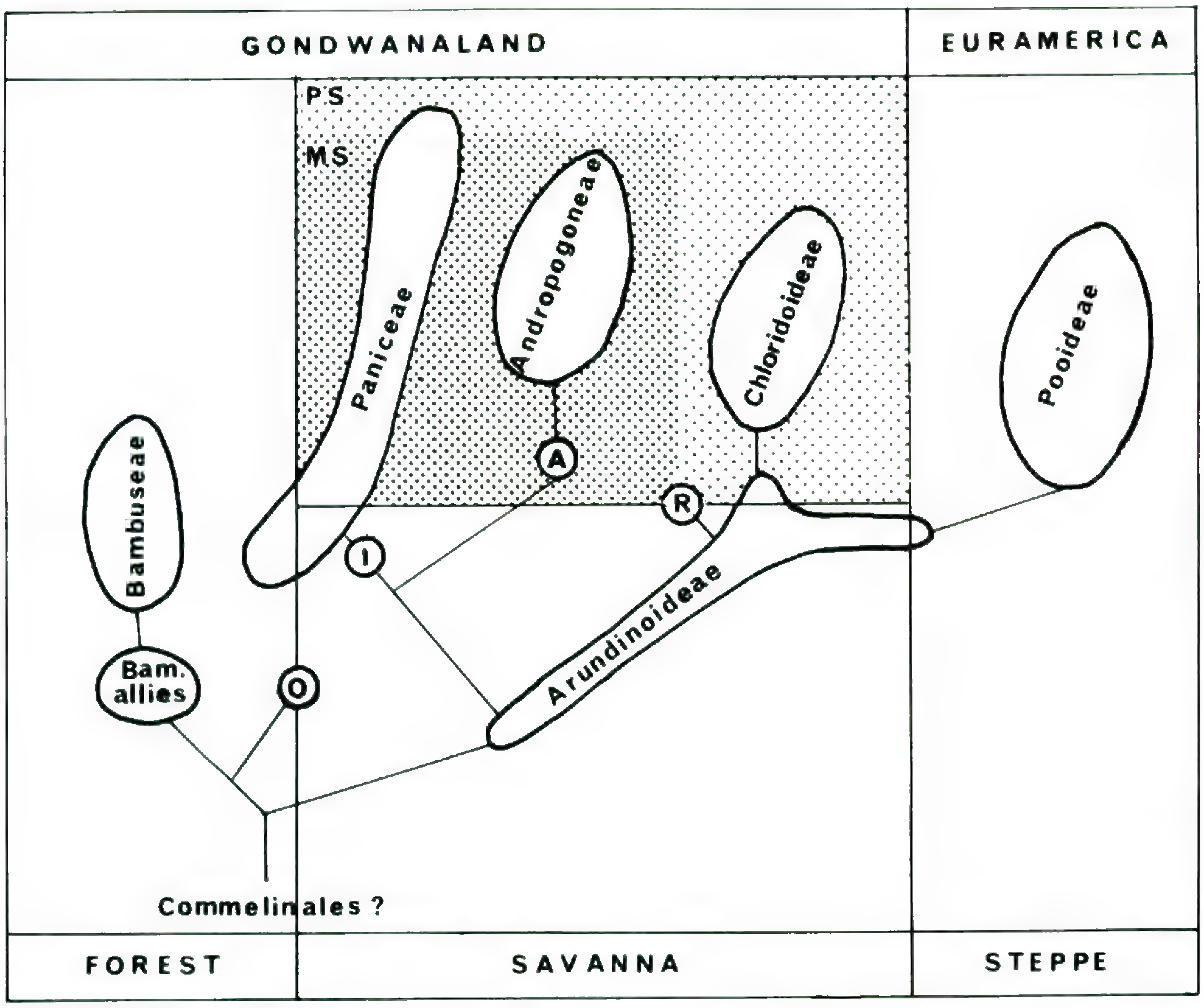

FIGURE 1. Suggested relationships among the major groups of grasses. A = Arundinelleae, I = Isachneae, O = Oryzeae, R = Aristideae. C_4 metabolism is indicated by stippling; it is divided into the MS and PS types of Brown (1977).

speculation is no bad thing provided we understand it to be no more than a working hypothesis, which gives coherence to a complex web of detail and grants some insight into the probable processes at work.

PHYLOGENY

We know, from the doctrine of evolution, that similarity between organisms is not accidental, but is due, in the first instance, to the chain of inheritance that links them together. We cannot determine this genealogical tree directly, but a good natural classification maps degrees of overall similarity, and should therefore contain sufficient information for us to deduce the main outlines of phylogeny. Let us then look at our classification in this light (Fig. 1).

The origin of the grasses is unknown, but most authorities relate them to the Commelinales in general and the Flagellariaceae in particular; at the very least there seems to be agreement that the most likely relatives are to be found in the tropical forests. Now the Bambusoideae, a subfamily defined by certain anatomical peculiarities such as fusoid and arm cells, is both tropical and primitive. Primitive in the sense that some genera have incomplete suppression of axillary

buds in the inflorescence and spikelets, and the flowers may retain trimerous symmetry. Among them is a group of small tribes (e.g., Olyreae) known as the bamboo allies, which paradoxically combine the primitive and baroque. This collection of curios, apparently the relics of ancient departures from the mainstream of grass evolution, gives some hint of the diversity that must once have existed in the ancestral stock. They are mostly insignificant broad-leaved inhabitants of the rainforest ground layer, which are often mistaken for other forest families such as Zingiberaceae. By contrast their near relatives the true bamboos have become successful competitors in this environment by developing woody tissue and adopting the form of trees. A flaw in this argument is the anemophilous pollen grain of all grasses (Page, 1978), for it seems incompatible with a forest origin. However, Oryzeae is a peripheral tribe of the subfamily, and its predilection for open marshland hints that the primitive habitat might have been glades and margins rather than the forest itself.

However, the future of the grasses lay, not in the forest, but in the tract between forest and desert that we know as savanna. The most likely candidates for the grasses which first moved into this environment belong to the subfamily Arundinoideae, for this is also primitive; primitive in the sense that it lacks distinctive features, but seems rather to represent the lowest common denominator of subsequent subfamilies. Its notoriously difficult taxonomy suggests that it is now reduced to dismembered fragments around a core which has become extinct.

Subfamily Chloridoideae is easy to place for it abuts onto Arundinoideae, and indeed the boundary between the two is difficult to establish. It ushers in a new development, the Kranz syndrome. This is a set of anatomical characters associated with C_4 metabolism, in effect an extra loop in the photosynthetic cycle (the basic form of which is known as C_3), that renders it more efficient in high temperatures (Teeri & Stowe, 1976; Tieszen et al., 1979).

Subfamily Panicoideae presents more problems. It has also evolved the Kranz syndrome, in fact two different versions of it (the MS and PS types of Brown, 1977), but some genera of Paniceae still retain the older non-Kranz anatomy and C_3 metabolism. Moreover, there are no direct links between the main tribes, Paniceae and Andropogoneae. The situation is still rather confused, but a tentative arrangement is shown in Fig. 1.

Finally, subfamily Pooideae seems to represent a new venture for the grasses, an adaptation to cold climates and invasion of the temperate steppes. It has retained the primitive C_3 pathway, for the more advanced form offers no advantage in a cool climate. This suggests a relationship with Arundinoideae, a few of whose genera have shown their ability to penetrate deeply into the temperate zone.

The Time Scale

Phylogeny would be simple if the sequence of events could be dated, but unfortunately the fossil record of grasses is exceedingly meager. However, there are some scraps of evidence relating to three main phases in the development of the grassland ecosystem.

The broad-leaved bamboo allies are a very minor constituent of the forest

ground layer and the woody bamboos themselves are thought to have been a later secondary adaptation. Therefore, whether we regard the closed rainforest as a cradle or museum, the grasses are unlikely to have been of much significance until they established themselves under the lighter canopy of marginal woodland, and assumed something approaching the familiar narrow-leaved life form. We may tentatively associate the onset of this process with the Paleocene, when unambiguous grass pollen first appears in the record (Muller, in litt.). Thereafter the unique potential adaptability of their life form, with its basal tillering, structural combination of stem and sheath, intercalary meristems and substitution of leaf sheaths for the floral envelope, enabled the grasses to move into progressively drier and more open habitats, securing an increasingly important role in the understory of the low interrupted tropical woodland and bushland which presumably occupied this environment. Development of the distinctive savanna physiognomy was aided by fire, for fires started by lightning seem always to have been a feature of the savanna environment (Komarek, 1972); burning is certainly of long standing for the savanna trees have evolved a number of distinctive fire-resistant features. Equally certainly the grass life form is unharmed by fires which destroy many of its competitors. In fact, savanna is an ecosystem in which grass provides the fuel that ensures its own survival.

The second phase of development followed the introduction of herbivores to the system. Contemporary grass-eating mammals have high-crowned teeth resistant to the abrasive properties of the silica bodies in grass leaves, and such teeth first appear among fossil mammals of the Middle Oligocene (Gregory, 1971; Webb, 1977). It can be inferred that grassland had emerged as a vegetation type by this time, and that grasses were undergoing further modifications to mitigate the effect of predation. The mammals responded by reciprocal adaptation, and in doing so they achieved a kind of symbiosis with the grasses, which were able to attract and sustain a level of grazing pressure sufficient to cripple their competitors. The Oligocene also provides the first grass fossils, some spikelets identified as *Stipa* (MacGinitie, 1953), indicating that at last some modern genera were extant by this time.

The third phase was the association of the grasslands with man, who extended and transformed them to support his grazing herds, and to provide the cereal crops upon which he relies so heavily for subsistence. This phase is documented in the archaeological record, but is not germane to the present discussion.

The main point to emerge from the scanty fossil record is that grasses were in existence during the early Tertiary when the continents were in the final stages of separation, and that their history must take this factor into account. The position of the continents at this time has been discussed in detail by Raven & Axelrod (1974) and Raven (1979), but the salient points may be summarized very briefly as follows. Africa and South America were some 800 km apart in the Paleocene, though there were probably intermediate oceanic islands, and moving gradually towards their present separation of 2,500 km. Madagascar-India was already separated from Africa; India parted company with Madagascar in the Paleocene, meeting Asia in the Middle Oligocene. There were probably feasible indirect routs for seed dispersal between Africa, Eurasia, North America and South America during most of the first half of the Tertiary. In addition there was

a direct temperate climate connection between South America, Antarctica and Australia until the Eocene (the connection between South Africa and Antarctica was severed in the late Cretaceous).

Beyond these snippets of fossil evidence, we must make what we can of a kind of fossil that is still available to us, and that is the present-day distribution of grasses.

The Distribution of Subfamilies

Hartley (1958a, 1958b, 1973) and Hartley & Slater (1960) have produced a series of maps showing the distribution of tribes and subfamilies. Their findings may be briefly summarized as follows:

Paniceae.—Tropical, humid equatorial zone; center in South America.
Andropogoneae.—Tropical, seasonal rainfall zone; centers in India and Southeast Asia.
Chloridoideae.—Tropical, particularly the dry belts of Cancer and Capricorn.
Pooideae.—Temperate, mainly northern but also in South America.

Hartley took his data from a large number of published Floras, calculating the percentage contribution which each group made to the total grass flora. This has the advantage that there is no pressing need to reconcile differences in taxonomic treatments between the various Floras. It yields a useful measure of relative importance, but percentages can sometimes be misleading. Cross (1980) has produced a set of maps using simple species counts, which reveal a number of discrepancies between tribal distribution measured by species abundance, and Hartley's method of relative importance. For example, the Pooideae have a high percentage figure in the north temperate zone where they are undiluted by other groups, but are actually most prolific in the Mediterranean region. She provides additional data on Bambusoideae (tropical) and Arundinoideae (southern subtropical).

From the foregoing it is evident that the major taxa have sorted themselves into worldwide climatic belts. Most of these are more or less sympatric in the tropics, but the Pooideae are radically different, having a predominantly north temperate distribution, and the Arundinoideae display a southern subtropical, possibly relict (Darlington, 1965), pattern. In short there are no surprises, for the distribution of major taxa is entirely consistent with taxonomic prediction.

Distribution of Genera

To examine this problem the world was divided into 25 areas, and the grass genera scored as present or absent in each. The resulting data matrix was then sorted by cluster analysis (Clayton, 1975).

Disregarding 87 genera whose distribution was essentially worldwide, there were found to be seven clusters of continental extent which together accounted for 450 genera. The remaining 98 genera were shared in various ways between adjacent clusters; some of these genera may have been naturalized introductions (known adventives were excluded from the outset), but well over half were represented by different species in the two parts of their range. They linked the

clusters into two chains: Eurasia, North America, temperate South America; and tropical America, Africa, tropical Asia, Australia.

The two chains are predictable, and strengthen the view that Pooideae are geographically distinct from the rest of the family. However, the discovery that two-thirds of the genera are confined to single continents is disturbing, for it demonstrates that genera are poor travellers, and raises the question of how the subfamilies achieved their worldwide distribution.

The ability of grasses to cross short stretches of sea is not in doubt, but there is no reliable evidence either way on the subject of longer journeys. Transoceanic voyages are certainly very difficult, for most of the wind or water currents have a sufficient north-south component to carry the disseminules into a different climatic zone, and the problem of establishing themselves in the face of native competition is known to be formidable. Moreover the rapidity with which numerous weedy grasses are becoming naturalized in alien territories strongly suggests that these plants, though admirably equipped for dispersal, could not cross the oceans until modern commerce provided a vector.

Of course, the vegetation of oceanic islands testifies that disseminules do arrive by some means or other. However, their flora is usually conspicuously unbalanced by comparison with the mainland, showing clear signs of derivation from a limited number of haphazard immigrants. There is no evidence of this phenomenon if we compare the grass floras of continents. To the contrary, they seem rather broadly based; the major subtribes of Andropogoneae, for example, show much the same pantropical distribution as the tribe itself.

It can also be argued that the low probability of successful transoceanic dispersal may have been offset by the enormous time span available. This proposition can be partially tested, for it implies that the older tribes have the best chance of achieving a wide distribution, and should therefore contain proportionately more of the 87 widespread genera. In fact the reverse is true; the tribes believed to be younger contain a higher proportion of widespread genera. It seems that the distribution of the older tribes is conditioned by their rate of extinction, rather than their rate of dispersal.

The inconsistency between the worldwide distribution of higher taxa, and a demonstrable reluctance of genera to cross the present day oceans, can be resolved by invoking continental drift. It is envisaged that the tropical subfamilies spread across the world during the first half of the Tertiary, the greatest water gap being some 1,200 km across the Atlantic; formidable enough, but nothing like such a strain on plausibility as the present width of the ocean. The older Arundinoids were driven outwards by the greater photosynthetic efficiency, in tropical latitudes, of the newer Kranz subfamilies. In the north temperate zone they gave rise to the Pooideae, and were all but replaced by them, the Pooids subsequently dispersing southwards along mountain chains. In the south temperate zone the Arundinoideae have survived, reaching Australia (together perhaps with some cool tolerant Kranz genera) via Antarctica. During the latter half of the Tertiary genera continued to evolve, but in comparative isolation upon the increasingly separate continents.

It is of interest to note that on the average widespread genera are much larger than single-continent genera, an obvious consequence of the larger area involved.

But they are still significantly larger when calculated on a species per continent basis, an effect presumably related to their greater age. The contrast between large and small genera suggests that two evolutionary strategies may be involved; the surviving, and by implication successful, older genera securely entrenched in their preferred environments which they exploit by complementary speciation, while the younger genera explore new and possibly labile environments by competitive replacement.

Distribution of Species

Species distributions are commonly demonstrated by means of selected examples. Whether the patterns found are applicable to the bulk of the species is left open to conjecture, but there is sufficient of a probabilistic element in plant distributions to cast suspicion on small samples. It is clearly better to work with very large samples, such as the whole of the Gramineae, but this is beset by three main problems.

Firstly, there is the matter of taxonomy, for little faith can be placed in results if the species themselves are in a state of taxonomic or nomenclatural confusion. Fortunately the grasses have attracted more taxonomic attention than any other family of comparable size, and we are now in a position to put together a tolerably accurate catalogue for most of the world except South America. Another facet of this problem is that it is sometimes very difficult to decide whether a species should rightfully be included as a native or not.

The second problem stems from interrelationships between the distributions of species, of habitats and of communities. This is largely a matter of scale, depending on the purpose of the investigation. The present intention is not to examine the ecological sorting of species into communities under the influence of local habitat factors, but to look beyond this to the overall species pools from which these communities are recruited. The sampling unit should therefore be fairly large in order to find the major patterns, while averaging out the finer detail. It has to be assumed that a full spectrum of habitats is repeated within each of these units, a reasonable assumption insofar as the common catenary sequence of soil types is concerned, but not altogether true of unusual habitats.

Thirdly, there are difficulties caused by the large number of species involved, and the often rudimentary nature of available distribution records. The problem becomes more tractable if data collection is inherently simple.

The method adopted was borrowed from ecology, and consisted of scoring each species as present or absent in "quadrats" of country size. The resulting data matrix was first sorted by cluster analysis (a minimum spanning tree), and then refined by inspection. It was satisfying to find that so crude a method actually worked, and that the results were fairly robust even when quite large adjustments were made to the data.

It was found that species are not arranged in a random mosaic, but are superimposed to such an extent that a limited number of generalized patterns suffice to describe their distribution; it seems likely that this is because they have become entrained with the dominant life form of the major vegetation formations. The individual distributions are not coincident but concentric, as might be expected

from the differing degrees of adaptability that exist between species. Consequently the cumulative patterns (phytochoria) have no definite boundaries, but fade away gradually at the edges, and are best mapped by some form of contouring. They also tend to overlap each other to a greater or lesser extent, an effect which may be exaggerated among grasses, which have a great capacity for infiltrating the seral stages of neighboring formations from which competition would otherwise exclude them. Nevertheless, it is important to appreciate that phytochoria do not have mutually exclusive territories in the manner of ecological communities; indeed, the latter are often synthesized from the members of several transgressive floristic elements.

Another feature of species distributions is that two or more subsets may rest within the geographical limits of a wider pattern, thus affording the basis for a heirarchical classification. Three principal categories are usually recognized:

Kingdom. Generally corresponds to the major land masses, and reflects the effect of continental isolation.

Region. Generally corresponds to the major vegetation formations, and reflects the effect of climatic differentiation.

Domain. In many ways the most interesting category, for it often bears little relation to ecological factors, but seems instead to represent a legacy of disequilibrium left by past historic events, notably the disruptive effect of climatic changes during the Pleistocene.

Regional studies have been made by Clayton & Hepper (1974), Clayton & Panigrahi (1974) and Cope (1977). These have subsequently been consolidated in a series of maps showing the distribution of grass species throughout the Old World (Clayton & Cope, 1980a) and in North America (Clayton & Cope, 1980b).

THE AFROMONTANE GRASSES

In working out the distribution of species it has been tacitly assumed that the floras of contrasting, but adjacent, habitats are not distributed independently. This proposition can be tested on data from the African mountains, for it is widely held that the flora of these high islandlike habitats is distributed differently from that of the surrounding lowlands, and constitutes a distinct Afromontane Region. However, when the grasses of the highland Afromontane Region (Clayton, 1976) and lowland Ethiopian Domain (Clayton & Cope, 1980a) are compared, they are found to have much the same geographical extent. There is thus evidence to suggest that the factors determining the present limits of these two floras have been broadly similar, despite the manifest difference in habitats, and that the geographical case for separating them is weak.

Separation of the Afromontane Region has been strongly influenced by the taxonomic affinity of its flora to temperate genera, implying that its original source was quite different from that of the surrounding tropical lowland flora. Presumably its precursors entered from the north. The precursors of the South African montane flora, of similar taxonomic affinity, must have passed along the same route, but the two floras are now represented by quite different species. They have evidently been evolving in situ for a considerable time and their ultimate

origin is not particularly relevant to their present distribution. Although evidence from taxonomic relationships is a valuable aid to understanding the past, it is often associated with an extended time span. We should therefore be wary of accepting it in the same context as the, largely Pleistocene, events which have shaped the boundaries of present-day phytochoria.

ENDEMIC SPECIES

Endemic species have always had a particular fascination for phytogeographers, and they are frequently invoked as a guide to the center of origin of genera of even whole floras. However, when endemics, in the sense of species confined to a single country, are plotted on a map (Clayton & Cope, 1980a), they are found to be surprisingly common. Evidently the notion of a limited number of compact endemic centers cannot be entertained. In fact, endemics are most abundant in the southern tips of continents, where isolation is probably a major factor. But they are also frequent in all the major orogenic zones (the flat pediplain of the Congo-Zambezi watershed is a notable exception), and there is a low background count almost everywhere.

It seems that we are confronted with two contrasting environments. The mountains offer a great variety of niches, and can accommodate a wealth of species; moreover, they are buffered against the worst effects of climatic change, for the vegetation can adjust by shifting its altitudinal zonation upward or downward. On the other hand, the plains offer a relatively uniform environment where evolution proceeds by competitive replacement, and where climatic change entails a major disturbance.

In short, the distribution of endemics gives little support to simplistic interpretations in terms of centers of origin or refugia. Certainly the species-rich mountains may constitute a valuable reservoir of genetic diversity, but it is likely that evolution has proceeded just as rapidly on the plains, though leaving no relicts to mark its course.

Conclusion

The history of the grasses is not a simple matter, for it is compounded from the evolutionary thrust of competition, selection pressures exerted by the environment, the degree of isolation imposed by shifting geographical configurations, and disruptive migrations induced by climatic change. Nor is it amenable to a wholly deterministic approach, for many of these factors operate in a probabilistic fashion. Nevertheless, I have tried to show that a coherent story can be pieced together from existing knowledge of taxonomy and distributions. I should emphasize that it is but a working hypothesis, for there are all too many gaps that must, for the moment, be bridged by conjecture rather than fact.

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SOME EVOLUTIONARY TRENDS IN THE BAMBUSOIDEAE (POACEAE)[1]

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ABSTRACT

Bamboos, which have woody culms, and several genera with herbaceous culms share a similar type of leaf anatomy and epidermis. Various other morphological features, including a distinctive type of seedling, also indicate a close relationship that supports the grouping of these genera together into a single subfamily, the Bambusoideae. A review of the chromosome numbers in the subfamily reveals that the herbaceous members are mostly diploid while the woody ones are polyploid, with $x = 12$ the basic number. Such evidence corroborates the hypothesis that bamboos have been derived from herbaceous ancestors. Most bamboos flower infrequently and have had far less opportunity for floral evolution than have the herbaceous members, which flower continuously or at least seasonally. The most primitive inflorescences have therefore been retained in the bamboos while highly specialized ones have developed in the herbaceous members. A knowledge of the former type of inflorescence is useful in an interpretation of the latter. With this in mind, the inflorescence of the herbaceous bambusoid grass, *Streptochaeta*, has been reexamined. This genus has long been considered to be the most primitive grass, in great part due to the presence of three large structures in the spikelet, thought to be primitive lodicules and two structures interpreted as a primitive, two-parted palea. Comparison of *Streptochaeta* with other members of the Bambusoideae suggests that the spikelet in fact lacks both lodicules and palea and that these structures represent instead bracts on different axes of a highly modified pseudospikelet. Such a pseudospikelet is comparable to that of a bamboo. While *Streptochaeta* may be considered primitive in its herbaceous nature and possession of a pseudospikelet, it must be regarded as advanced in other features, among them the lack of lodicules. No one member of the subfamily can be considered most primitive. The least advanced inflorescences are retained in bamboos, such as *Bambusa*, while the most primitive growth form occurs in herbaceous genera like *Streptochaeta*, *Streptogyna*, and *Pharus*. The significant trends of evolution within the subfamily become apparent, however, only when all of the genera—woody and herbaceous—are considered together. The bambusoid line—with its complex leaf anatomy and epidermis—is itself specialized and not to be regarded as the precursor of the other groups of grasses.

The major, large, natural groups of grasses can be determined by relatively few factors that are of basic importance in the family, among them the internal structure of the leaf and features of the leaf epidermis and embryo. Other characters, such as chromosome number and seedling type, in correlation with these result in the recognition of six or seven major groups that most agrostologists agree upon as being natural. These are commonly known as the arundinoid (phragmitoid), bambusoid, centostecoid, chloridoid (eragrostoid), oryzoid, panicoid, and pooid (festucoid). Often these groups are called subfamilies. Odd genera here and there have sometimes been considered of equal importance so that in the literature we find whole subfamilies based upon single genera: Anomochlooideae and Micrairoideae are examples.

The bambusoid group is best known by its Gargantuan members, the tree grasses, such as *Dendrocalamus giganteus* of northern Burma, whose culms may

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[1] The illustrations, except for Fig. 7, were prepared by Alice R. Tangerini, to whom I am indeed indebted for her skillful rendition of a multitude of new and often difficult structures. Figure 7 was drawn by Mrs. Gesina Berendina Threlkeld as part of a series of illustrations of Ceylonese bamboos, to be published as a unit at a later date.

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reach 30–35 m in height and 25–30 cm in diameter. The clumps of such bamboos reach enormous proportions and the plants are known for their propensity to continue growing vegetatively, even for decades, before they flower. Size, complexity of body, and rarity of flowering have contributed to the neglect that bamboos have received from systematists and the taxonomic confusion that has long plagued them. Not all bamboos, however, are so large as *Dendrocalamus*. At the other end of the scale we find *Arundinaria pygmaea*, whose wiry culms reach no more than half a meter in height, but like the bigger members also branch at the nodes and flower seldom.

Regardless of size, both *Dendrocalamus* and *Arundinaria* share a number of features that are common throughout the bamboos: a specific type of leaf anatomy and epidermis; distinctive seedling; flowers with three lodicules, often six stamens, and three stigmas; and fruit with a small embryo and linear hilum. Many other grasses of small stature that inhabit shaded forests also possess these basic features, which demonstrate a natural relationship. Besides their smaller stature, they do not have such complex branching as the bamboos nor such long-lived culms, and they commonly flower throughout the year or at least seasonally. These grasses, with the bamboos, constitute the subfamily Bambusoideae.

We refer to the one group of Bambusoideae as "herbaceous bambusoid grasses" and to the other as "woody bambusoid grasses," or simply bamboos. When we speak of "woody," we mean this in the sense of being hard, not like the stem of a dicotyledonous tree that produces secondary xylem. The bamboo culm is characterized by collateral bundles embedded in parenchymatous tissue, with the bundles toward the inside more separated from one another than those toward the periphery, which are smaller and occur very close together. A cap of fiber strands usually occurs on both sides of the bundle, and this abundant sclerenchyma in the culm, along with thick-walled and lignified ground tissue, accounts for the hardness of the culm. Some additional strengthening may be contributed by the silica that is present in the epidermis. Detailed studies on the anatomy of the bamboo culm have been carried out by Grosser and collaborators (Grosser, 1970; Grosser & Liese, 1971; Grosser & Zamuco, 1971).

All bambusoid grasses grow in association with woody vegetation and are never components of prairies or grasslands, being most common in temperate woodlands or tropical forests or, if herbaceous, in the shaded understory of warm forests. They are usually dependent on humidity, at least during the growing season; those few that grow in drier regions or areas with a dry season may lose their leaves during this period. Bambusoid grasses are most abundant in the world's tropics and subtropics, but a few members are found in temperate-cold areas of both hemispheres. They occur between 46° north latitude and 47° south latitude and from sea level to as high as 4,000 m elevation, and are found on all continents except Europe. The bambusoid grasses represent the most widespread and diverse assemblage of genera and species within the family. So distinctive and natural is the group that Tzvelev (1976), in his recent system of classification of grasses, recognized it as one of his two subfamilies, the other being the Pooideae. Following are some of the basic characteristics of the Bambusoideae, a more detailed elaboration of which is given in Calderón & Soderstrom (1980).

Bambusoideae

General morphology: perennials, herbaceous or woody, rhizomatous; culms when woody branched at the nodes; leaf blades usually flat, broad, lanceolate or linear-lanceolate, articulate with the sheath by a petiole that orients the blade in different positions; blades with tessellate venation strongly or weakly manifest; flowering seasonal or occurring infrequently; inflorescences of different types, often of complex systems of partial inflorescences of limited branching or unlimited branching and production of spikelets or pseudospikelets; spikelets or pseudospikelets 1–many-flowered, without glumes or with 1–several "transitional" glumes; lemmae 3–many-nerved, awnless or only seldom awned and then the awn not geniculate; palea 2–many-nerved, keeled or rounded dorsally, exceptionally bifid; lodicules generally 3 (0–6, rarely many), usually large and with hairs of different types and well-developed vascularization; stamens 3–6 (rarely 2, occasionally many), sometimes partially fused or monadelphous; stigmas 2 or 3; fruit usually a caryopsis, sometimes an achene or fleshy; hilum linear, almost as long as the fruit; embryo small in comparison to the fruit.

Seedling: coleoptile usually short and not elevated from the caryopsis; first one to several leaves usually bladeless or with a reduced blade; first expanded blade usually broad, ovate or lanceolate, horizontal in position.

Leaf anatomy: leaf blade with a conspicuous midrib containing a complex vascular system of several bundles in 2 rows, strongly developed sclerenchyma and ground tissue; mesophyll with cells arranged in horizontal layers parallel to the epidermis, not radiate; chlorenchyma composed of arm cells and translucent fusoid cells at each side of the vascular bundle and in between layers of arm cells; bundle sheaths always double and well developed, the outer sheath with very few chloroplasts; transverse veinlets connecting the longitudinal vascular bundles.

Leaf epidermis: with short cells in pairs or sometimes in rows over the veins; silica bodies usually cross shaped, saddle shaped, of olyroid type or of intermediate forms; microhairs nearly always present, bicellular with both cells of about the same length and with a rounded apex, or sometimes of 3 or 4 cells, papillae common and abundant on the long cells and overarching the stomata; long cells with thick, sinuous walls; stomata usually with low dome-shaped or sometimes triangular subsidiary cells.

The herbaceous bambusoid grasses, which are fewer in number than bamboos but have received more attention in recent years, are more clearly understood than the bamboos. We are able to delimit the genera of herbaceous bambusoid grasses and are able to recognize related groups of genera, or tribes. While this is also true for some bamboos, for the most part generic limits are still poorly understood and consequently tribes are not yet recognized for most.

We presently recognize eight tribes of herbaceous bambusoid grasses, the following six occurring in the American tropics: Anomochloeae, Olyreae, Parianeae, Phareae, Streptochaeteae, and Streptogyneae. Only two of these are represented outside of the Americas. The Phareae contains two genera, *Pharus* of the American tropics and *Leptaspis* of the Old World tropics, and the Streptogyneae is monotypic, with one species of *Streptogyna* occurring in the New

World and one species in Africa, southern India and Ceylon. The other American tribes vary in size, with the Anomochloeae and Streptochaeteae each monotypic (*Anomochloa* and *Streptochaeta*), the Parianeae with two genera (*Eremitis, Pariana*), and Olyreae with 15 (*Arberella, Cryptochloa, Diandrolyra, Ekmanochloa, Froesiochloa, Lithachne, Maclurolyra, Mniochloa, Olyra, Piresia, Raddia, Raddiella, Rehia, Reitzia, Strephium*). A key to the herbaceous American tribes appears in Calderón & Soderstrom (1980).

The tribe Atractocarpeae is represented only in Africa, and contains the genera *Guaduella* and *Puelia*, while the monotypic tribe Buergersiochloeae is known only from the genus *Buergersiochloa* in New Guinea. The herbaceous bambusoid grasses are most abundant in the New World where they reach their greatest diversification and comprise well over one hundred species, many still undescribed.

There are 17 described genera of bamboos in the New World alone, of which only two occur in Asia, *Arundinaria* and *Bambusa*. The others are all endemic to the American continent. An equal or greater number of bamboo genera occur in the Old World, with many endemic to Madagascar, surpassing the number that occur in all of Africa.

The trends of evolution in the subfamily become apparent only when we study all the genera together, herbaceous and woody. Previous systems of classification have often obscured these patterns, for the woody genera were placed in a single tribe, Bambuseae, and the herbaceous genera were scattered in widely unrelated tribes, such as the Hordeae and Paniceae, that pertain to other subfamilies.

A survey of many bambusoid seedlings shows that they are of an unique type, with certain features not found in the seedlings of other grasses. The fact that the seedlings of both herbaceous and woody members are similar strengthens the argument that these genera are closely related, which corroborates the conclusions based on studies of the leaf anatomy and epidermis.

The development of the woody habit and emphasis on vegetative reproduction in the bamboos has been accompanied by a decrease in flowering. Most bamboos bloom only at long intervals, these sometimes as much as 120 years. This has in effect prevented gene interchange in bamboos and arrested evolution of the inflorescence. On the other hand the herbaceous members, which bloom throughout the year or at least seasonally, in comparison with the bamboos have had countless generations of flowers and continuous opportunity for evolution of the flowering system. Among the herbaceous members, we therefore encounter highly specialized inflorescences and spikelets while in the bamboos we find them to be more primitive and less specialized.

The herbaceous bambusoid genus, *Streptochaeta*, long considered to be the most primitive of all grasses, can now be reinterpreted in light of the above ideas. A study of its seedlings confirms that the genus is bambusoid. A knowledge of chromosome numbers in the subfamilies suggests that the somatic number of $2n = 22$ in this genus represents a diploid based on a derived basic number. Analysis of the so-called spikelet of the genus and comparison of it with the inflorescence of a primitive bamboo reveals that the flowering unit is in fact a highly modified pseudospikelet.

While *Streptochaeta* does indeed have primitive features, our study of other

bambusoid seedlings and chromosomes shows that two other genera must also be primitive. These genera, *Streptogyna* and *Pharus,* have peculiar, apparently undifferentiated, seedlings, and are diploids, based on the primitive number of $x = 12$. Their present-day distribution also points to an archaic existence, for one species of *Streptogyna* occurs in the New World and one in the Old World. *Pharus* is represented in the New World by several species and its sister genus, *Leptaspis,* is represented by several species in the Old World.

The herbaceous bambusoid genus, *Puelia,* which is endemic to Africa, also is a diploid based on $x = 12$. We thus find a concentration of primitive herbaceous types in present-day tropical Africa, with the most highly specialized herbaceous genera in the New World. The polyploid bamboos, which are apparently derived from herbaceous ancestors, occur in the Old and New World alike. The highest polyploid bamboos, however, are found in Asia.

The Bambusoid Seedling (Figs. 1–3)

Studies of the embryo in grasses have been so numerous and interpretations of the component structures so diverse that a voluminous literature exists. The reader is referred to Brown (1960), who reviewed the major papers and interpretations of each author. I do not, however, agree with the conclusions that he personally drew. His paper was followed in close sequence by at least two others that do not agree with his findings either: these are Guignard (1961) and Negbi & Koller (1962).

The grass embryo is of special interest because it has unique structures whose homologies have been the subject of much debate. Most studies have been made on cultivated grasses such as wheat (*Triticum*) and maize (*Zea*), an unfortunate situation as these grasses have been so modified by man. I agree with Reeder (1953) who felt that more primitive grasses should be used for study of these structures; he himself chose one, *Streptochaeta,* for his study of the coleoptile.

The grass embryo, together with the endosperm, and surrounding wall structures comprise the grass fruit, which is generally a caryopsis. In rare, specialized cases, such as the bamboo genus *Melocanna* (Stapf, 1904), the endosperm is lacking in the mature fruit and the pericarp, along with the scutellum, becomes fleshy.

We can imagine the grass plant in its earliest stages as an axis, the basic part being the embryonal axis with the main seat of differentiation the node where the scutellum is attached. We may call this the first node of the grass plant and it occurs within the embryo. The axis continues upward and the next node marks the origin of the coleoptile. These two nodes and the internode between them are important in our discussion as these structures are unique to grasses and not really comparable to embryos of other monocotyledons.

The scutellum is a flat organ that is specialized for absorption of nutrients from the food reserve or endosperm. It remains within the fruit as the other parts become visible at germination. Opposite the scutellum there is sometimes present, as a nonvascularized outgrowth, a structure called the epiblast. The coleoptile is a sheathing structure and is generally closed; it protects the growing apex of the embryo, which it completely encloses. At germination the growing apex, or plumule, pushes through it.

Below the point of attachment of the scutellum is an elongated zone of tissue, the radicle, enclosed in a sheathing structure called the coleorhiza. The coleorhiza terminates in suspensor cells.

The scutellum is generally accepted to be a cotyledon. For this reason the node where it is attached is called by some the "cotyledonary node," but I prefer the term "scutellar node," as employed by Avery (1930), as it is descriptive rather than interpretive. By the same reasoning Avery's term, "coleoptilar node," for the next node is appropriate. According to some authors (Negbi & Koller, 1962), the epiblast represents a second cotyledon. However, it may be nothing more than an outgrowth of the coleorhiza and, furthermore, it is not always present.

For practical purposes, since a scutellum and coleoptile are always present, let us use them as markers of the first and second nodes of the embryonal axis, the region in between being the first internode of the plant's axis as accepted by Avery. This internode is somewhat specialized, as we might expect, and each succeeding internode becomes anatomically more like those of the culm. Since the time of Čelakovský (1897), this region has often been referred to as the mesocotyl, an interpretive designation that relies on a theory that regards this as an elongated node belonging neither to epicotyl nor hypocotyl.

The plumule, enclosed within the coleoptile, consists of numerous nodes and internodes, the nodes bearing the embryonic leaves. Its axis is a continuation of the embryonal axis; its first internode, the one just above the coleoptile (which is the second internode of the axis), is called a "transition internode" by Avery since it has an anatomical structure intermediate between that of the first internode and the next higher one, the third. Upon germination the plumule elongates and pushes through the coleoptile, which is a closed sheathing structure that is generally two-nerved. The second internode may elongate greatly at this time, elevating the remainder of the plumule. At the same time the radicle elongates and pushes through the coleorhiza. Some authors consider the coleorhiza to be a modified primary root, especially since it terminates in suspensor cells, which are characteristic of that organ. If the coleorhiza is indeed homologous to the primary root, and this seems reasonable to me, the structure normally referred to as "primary root" is an adventitious one. To avoid the use of an interpretive term in identifying this structure that emerges through the coleorhiza, I am using the word "radicle."

The structure of the embryo, its size relative to the endosperm, structure of the starch, and type of seedling have all provided useful characters in grass systematics. The most important papers on this subject, especially the embryo, are those of Yakovlev (1950) and Reeder (1957, 1962).

Numerous publications by Kuwabara, commencing with his 1960 paper in English, have shown the systematic significance of grass seedlings, a topic discussed more recently in detail by Hoshikawa (1969). The latter author studied over 200 grass species in 88 genera and found that, as with embryo types, seedling types could also be used to delimit major natural groupings within the family.

Unfortunately, the terminology of Hoshikawa is not clear and is sometimes misleading. For example, the coleoptilar node (as I am using it) is referred to by him as the "cotyledonary node," a term often used for the first or scutellar node.

FIGURE 1. Seedlings of Bambusoideae.—a. *Aulonemia* aff. *aristulata*, Brazil, Espírito Santo, Linhares, *Soderstrom & Sucre 1901*.—b. Embryo of *Streptochaeta spicata* just beginning to emerge from fruit, Costa Rica, Puntarenas, Palmar Sur, *Pohl & Calderón 10089*.—c. *Streptochaeta spicata*, same collection as b.—d. *Lithachne pauciflora*, Puerto Rico, Mayagüez, *Soderstrom 1801*.—e. Detail of germinating fruit of *Lithachne pauciflora*, same collection as d.—f. *Ochlandra stridula*, Ceylon, near Anandara, *Soderstrom 2563*.

For the scutellar node he coins the term, "transitionary node." In spite of these drawbacks, his scheme is interesting and of value. He points out differences that are quite useful in differentiating seedlings, such as points of origin of adventitious roots and their relative rates of development, and elongation or suppression of the first internode (his "mesocotyl") and second internode.

Based on the study of seedlings of seven bamboo species, Hoshikawa (1969) defined the bambusoid seedling as follows, his terminology following mine in parentheses: the first internode (mesocotyl) does not elongate, adventitious roots are lacking from both the scutellar (transitionary) node and coleoptilar (cotyledonary) node, and the blades of the leaves (leaves) from the lowest nodes are entirely suppressed or are only weakly developed.

Unaware of this paper, Calderón and I (1973) defined the bambusoid seedling on the basis of an herbaceous genus, *Maclurolyra*. We stated that the coleoptile is short and not elevated above the caryopsis by an internode (i.e., the first internode does not elongate), the first two to several leaves lack blades or the blades are reduced, and the first expanded blade is broad, ovate-lanceolate, and horizontal in position. We also pointed out the similarity of bambusoid to oryzoid grasses in the presence of reduced blades in the first leaves of the new shoot, but that in the latter group the first expanded blade is linear and ascending rather than horizontal in position.

I have now examined the seedlings of several more herbaceous and woody bamboos, including the genera *Streptochaeta*, *Streptogyna*, and *Pharus*, all of which belong to different tribes and have been considered as archaic and related to bamboos. All of the seedlings were collected from beneath parent plants in the field, with the exception of *Streptogyna*. In that case I collected the fruits in Espírito Santo, Brazil, on 16 March 1972, and planted them in pots at the Jardim Botânico in Rio de Janeiro on April 13. Seedlings were collected at intervals of about one month and preserved in FAA (90 parts of 50 percent EtOH : 5 parts glacial acetic acid : 5 parts formalin).

The following descriptions of the seedlings (whether of herbaceous or woody genera, as indicated) may be compared with the illustrations that appear in Figs. 1–3.

SEEDLING DESCRIPTIONS

1. *Arundinaria gigantea* (Fig. 2f) — woody

A short coleoptile is followed by two sheaths and a leaf with a small ovate, more or less horizontal, blade.

2. *Aulonemia* aff. *aristulata* (Fig. 1a) — woody

The first and second internodes do not elongate; the coleoptile remains very short, followed by two short sheaths, a longer sheath, and the first leaf with a small, oval horizontal blade.

3. *Diandrolyra* sp. (Fig. 2e) — herbaceous

The short coleoptile is followed by two sheaths, and then a leaf with a small, horizontal, ovate blade.

4. *Lithachne pauciflora* (Figs. 1d–e) — herbaceous

In one seedling the coleoptile is short, followed by two sheaths, and a leaf with an ovoid-lanceolate blade horizontal in position. In the other seedling an

FIGURE 2. Seedlings of Bambusoideae.—a. *Pharus* sp., Brazil, Bahia, *Calderón 2171*.—b–c. *Raddia* sp., Brazil, Rio de Janeiro, *Soderstrom, Sucre, & Calderón 1858*.—d. *Olyra loretensis*, Colombia, Leticia, *Soderstrom 1429*.—e. *Diandrolyra* sp., Brazil, Rio de Janeiro, *Soderstrom & Sucre 1935*.—f. *Arundinaria gigantea*, USA, Maryland, *McClure*, bamboo garden introduction no. *2762*.

elongated portion precedes a node bearing some roots that pierce the coleoptile that covers it. Here it is the second internode that has elongated. The node bearing the first leaf is covered by the elongated coleoptile.

5. *Ochlandra stridula* (Fig. 1f) woody

The coleoptile is short, followed by two sheaths and then several closely overlapping sheaths, each bearing a small, more or less horizontal-ascending blade. Germination of a bud, apparently in the axil of the coleoptile, gives rise immediately to a second shoot similar to the first. Quick germination of further buds produces a miniature clump of new shoots at the seedling stage.

6. *Olyra loretensis* (Fig. 2d) herbaceous

The short coleoptile is followed by two sheaths without blades; the following leaf bears a small, ovate, more or less horizontally positioned blade.

7. *Pharus* sp. (Fig. 2a) herbaceous

The first internode does not elongate, the second hardly so or sometimes extending for some length, with the coleoptile elongating concomitantly. The third node produces a leaf with expanded blade, which is broad, ovate, and horizontally positioned, but without reduced blades preceding it.

8. *Raddia* sp. (Figs. 2b–c) herbaceous

The short coleoptile is followed by one leaf with a tiny erect blade and a second one with the first expanded blade, which is broad-lanceolate and horizontal.

9. *Streptochaeta spicata* (Figs. 1b–c) herbaceous

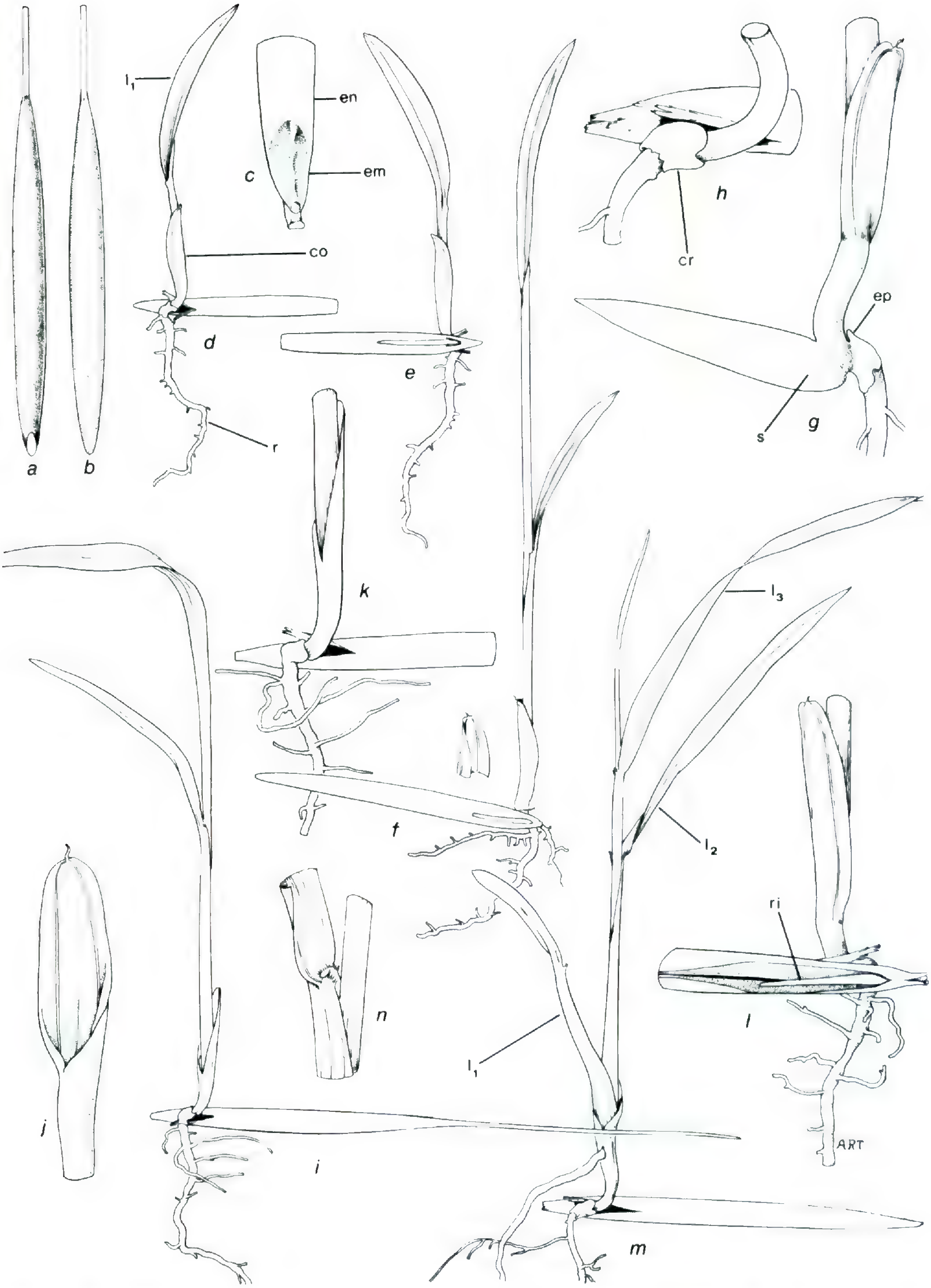
The first internode does not elongate; the second internode is very short. There are up to three leaves without blades or with reduced blades that precede the first leaf with an expanded one, which is broad and horizontally positioned. The short coleoptile is 5-nerved.

10. *Streptogyna americana* (Figs. 3a–n) herbaceous

The first internode does not elongate; the second internode elongates, as does the coleoptile. The third node produces a root and leaf with narrow, ascending, fully developed blade. There are no reduced blades nor is the first blade broad and horizontal. The basal portion of the coleoptile is thickened and appears to be fused to the second internode but careful dissection reveals them to be free from one another. There are two strong nerves in the coleoptile and sometimes a faint line that appears to be a median nerve, although this may only be an artifact. However, the coleoptile is mucronate, a condition not found in any of the other bambusoid grasses I have studied.

→

FIGURE 3. Fruit and seedling of *Streptogyna americana*.—a. Caryopsis showing relation of embryo (at base) to endosperm.—b. Caryopsis showing long linear hilum.—c. Base of caryopsis enlarged to show embryo.—d. Seedling 5–6 weeks old breaking through covering bracts, showing coleoptile (co), radicle (r), and first leaf (l_1).—e. Opposite side of d showing seedling in relation to the persistent rachilla internode.—f. Seedling 8 weeks old.—g. Detail of f at region of embryo emergence, showing the coleoptile, epiblast (ep), coleorhiza, radicle, and scutellum (s), covered by the pericarp.—h. Enlargement of g showing coleorhiza (cr).—i. Seedling 3 months old. The mature elongated style is shown here, but broken off or shortened in the other drawings.—j. Upper part of coleoptile of f. (×6).—k. Detail of i at region of embryo emergence.—l. Detail of i at region of embryo emergence, from side of persistent rachilla internode (ri).—m. Seedling 4 months old showing 3 developed leaves.—n. Ligule of first leaf of f. [Drawings a and b based on *Swallen 5089* from Obidos, Pará,



Brazil. The seedlings are all taken from plants cultivated at the Jardim Botânico, Rio de Janeiro, Brazil, from fruits collected by *Soderstrom & Sucre 1906* in Brazil, Espírito Santo, Reserva Florestal de Linhares, 16 March 1972. All fruits were planted 13 April 1972: d was removed at the end of May, f on June 14, i on July 16, and m on August 16.]

BAMBUSOID SEEDLING DEFINED

On the basis of published findings and the additional seedlings described here, we can make the following definition of the bambusoid seedling:

The first internode does not elongate; the second internode is usually short with the coleoptile remaining short, but occasionally it elongates with the coleoptile elongating as well; the first node or first several above the coleoptilar node bear leaves that lack a blade or the blade is reduced; the first expanded blade is usually broad, ovate-lanceolate and positioned horizontally; adventitious roots are usually lacking but may occur at both the scutellar and coleoptilar nodes; a bud may be produced at the coleoptilar node.

While this is a generalized description, we find that the seedlings of two genera in our study depart from this. *Pharus* and *Streptogyna* both lack reduced blades; in the former the first blade is expanded, large and ovate, and in the latter it is narrow and ascending.

The principal features of bambusoid grass seedlings then are the nonelongation of the first internode and general lack of roots at the scutellar and coleoptilar nodes. In the oryzoid and pooid grasses, for example, there is an elongation of the first internode and production of roots at the coleoptilar node.

CHROMOSOMES (Fig. 4)

Chromosome counts in the Bambusoideae are by no means numerous, yet there is a sufficient number to allow us to discern some general patterns and form some postulations. The following account is based on data from the literature and from counts made on plants that we have collected in the field or have in cultivation. In each case I am citing the single reference for the count, or a representative one when there are more.

The differences in somatic numbers in the Bambusoideae are great, ranging from $2n = 14$ in *Olyra fasciculata* (Morisset, in litt.) to $2n = 72$ in *Dendrocalamus giganteus* (Gould & Soderstrom, 1974). That the former is an herbaceous member and the latter a gigantic woody one is particularly interesting as, in general, the lower, diploid numbers are found in the herbaceous genera and higher, polyploid numbers in the woody.

A basic number of $x = 12$ is found in a few of the herbaceous bamboos and the tetraploid complement, $2n = 48$, among many of the woody bamboos. In diploid form, $2n = 24$, this number occurs in genera of three tribes of herbaceous bambusoid grasses: *Streptogyna* (Kammacher et al., 1973) of the Streptogyneae; *Leptaspis* (Tateoka, 1958) and *Pharus* (Pohl & Davidse, 1971) of the Phareae; and *Puelia* (Dujardin, 1978) of the Atractocarpeae. Hsu (1972) gave this number for two woody bamboos from Taiwan, *Bambusa oldhamii* and *B. stenostachya*.

The tetraploid number of $2n = 48$ occurs throughout the bamboos in widely unrelated taxa, such as *Arundinaria gigantea* (Gould, 1960) from the United States, *Neurolepis* (Gould & Soderstrom, 1970) from Andean South America, *Chimonobambusa* (Mehra & Kalia, 1976) from the Himalayas, *Indocalamus* (Janaki Ammal, 1945) of Ceylon, and *Shibataea* (Okamura & Kondo, 1963) from Japan.

Hexaploids of $2n = 72$ have been recorded for several woody bamboos, especially those largest in stature, including *Oxytenanthera abyssinica* (Reeder &

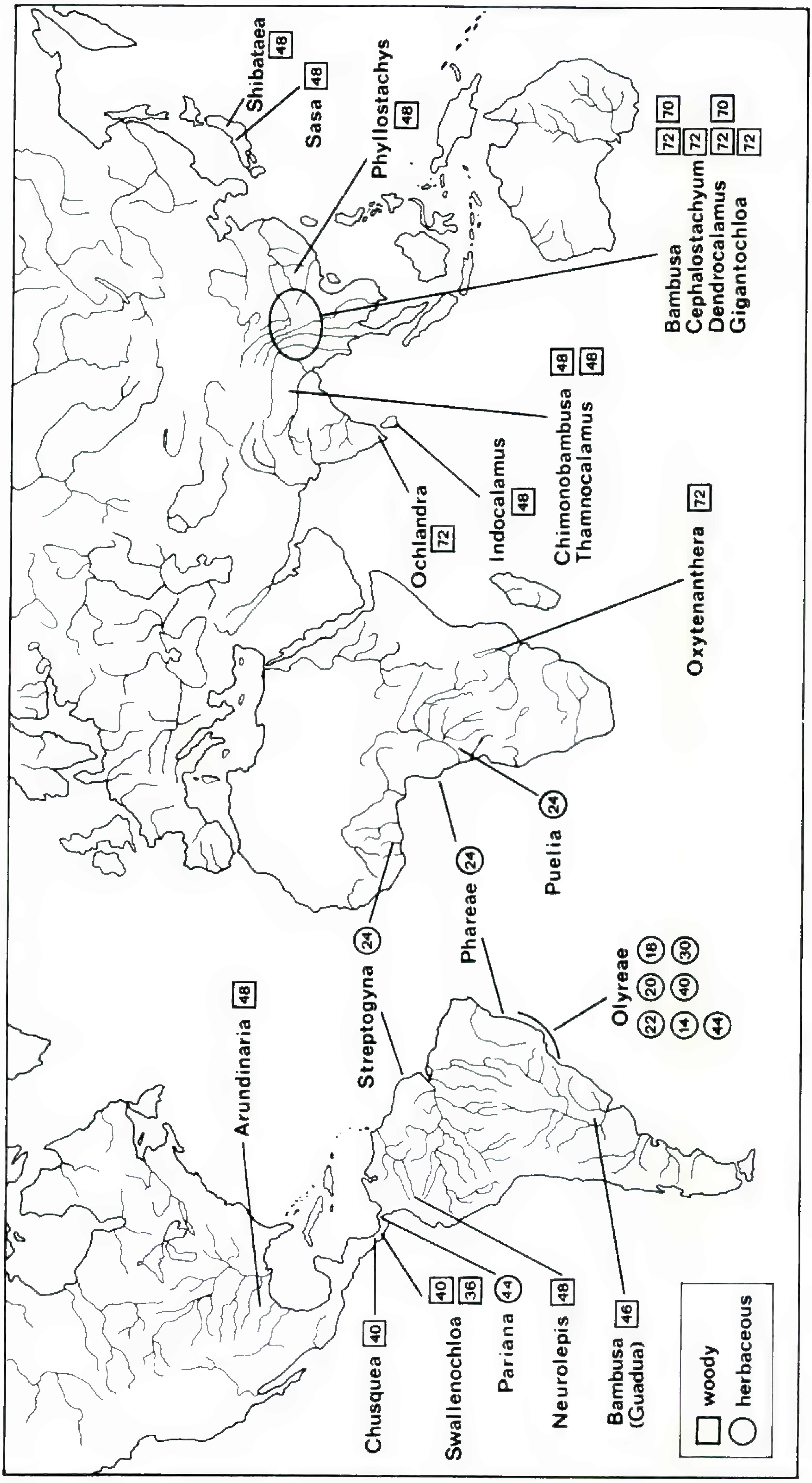


FIGURE 4. Chromosome numbers (2*n*) in the Bambusoideae.

Singh, 1967) of Africa and *Ochlandra* (Janaki Ammal, 1945) from India. However, there is a noticeable concentration of hexaploids in the mountains of northern Burma and western China. The hexaploid bamboos that are native to this region include *Bambusa polymorpha* (Janaki Ammal, 1945), *B. tulda* (Christopher & Abraham, 1971), *Cephalostachyum pergracile* (Sarkar et al., 1977a), *Dendrocalamus brandisii* (Janaki Ammal, 1945), *D. giganteus, D. hamiltonii* (Mehra & Sharma, 1972), *D. longispathus* (Janaki Ammal, 1945), *D. strictus* (Richarria & Kotval, 1940), and *Gigantochloa macrostachya* (Sarkar et al., 1977b). The hexaploid bamboos from this region include the largest species, *Dendrocalamus giganteus,* and some of the most widely planted and economically important, such as *Bambusa tulda* and *B. polymorpha*.

It is interesting to point out that Janaki Ammal (1950, 1954) found this region to contain the highest polyploid races of *Rhododendron* and *Buddleia*. Darlington (1973) speaks of this region, between the headwaters of the Yangtze and Salween rivers, as the most diversified and florally richest in the world. He feels that in colonizing new habitats in this territory new polyploid races and species are produced and survive in abundance. He regards this as a special situation in which extreme or peripheral ecological conditions confront the species in what is geographically the interior of its range.

In the New World we encounter interesting divergences from the pattern in the Old World. For example, the species of *Guadua,* now regarded as a subgenus of *Bambusa,* have a somatic number of $2n = 46$. This number has been found in three species of the subgenus so far examined: *B. capitata* (Gould & Soderstrom, 1967), *B. chacoensis* (Quarín, 1977), and *B. paraguayana* (Quarín, 1977).

We find divergences in the counts for the American bamboo genera, *Chusquea* and *Swallenochloa*. The expected tetraploid number of $2n = 48$ was given by Janaki Ammal (1959) for the species of *Chusquea* that she studied, while Pohl & Davidse (1971) found $2n = 40$ for the species of *Chusquea* and *Swallenochloa* that they examined. An even lower number, $2n = 36$, was reported by Virkki (1963).

The greatest variation of somatic numbers within a group occurs in the tribe Olyreae, which contains 15 described genera of herbaceous bambusoid grasses. The tribe is endemic to tropical America except for the single weedy species, *Olyra latifolia,* which has become naturalized elsewhere. Somatic numbers of 22 and 20 are the most common in the tribe, but 18 and 14 have also been reported, as well as 30, 40, and 44. A basic number of $x = 12$ has not been found in any member of this tribe.

In the genus *Olyra* itself we find $n = 11$ to be common: in *O. latifolia* we have diploids of $2n = 22$ (Davidse & Pohl, 1972a) and tetraploids of $2n = 44$ (Davidse & Pohl, 1974), while in another widespread weedy species, *O. micrantha,* we have only $2n = 40$ (Gould & Soderstrom, 1967). *Olyra taquara* is a diploid, with $2n = 20$, and *O. fasciculata* a diploid with $2n = 14$ (Gould & Soderstrom, 1967).

Other genera in the tribe include *Cryptochloa,* with a report of $2n = 22$ for *C. concinna* (Davidse & Pohl, 1974) and $2n = 20$ for an undescribed species (*Soderstrom 1380*) from Colombia (Gould in litt.). Other olyroid genera with a basic number of $n = 11$ are *Lithachne,* where both the diploid, $2n = 22$ (Pohl

& Davidse, 1971), and tetraploid, $2n = 44$ (Quarín, 1977), have been found; *Maclurolyra tecta*, $2n = 22$ (Calderón & Soderstrom, 1973); and *Piresia*, $2n = 22$ (Gould & Soderstrom, 1967). A basic number of 10 has been found in *Raddiella esenbeckii* (as *R. nana*) by Davidse & Pohl (1972b) and *Rehia* (as *Bulbulus*) *nervata* by Gould & Soderstrom (1967).

In the herbaceous tribe Parianeae, $2n = 44$ has been found for a species of *Pariana* (*Calderón & Dressler 2136*) (J. Hunziker, 1978, in litt.) and $2n = 22$ for *P. parvispica* (Pohl, 1972), which contrasts with a basic number of $x = 12$ implied in the $2n = 48$ count reported by Reeder et al. (1969) for *P. stenolemma*. In our own cultivated specimens of *Eremitis*, Royce Oliver (pers. comm.) has recently found the two species examined to be high polyploids, with somatic numbers over 60.

In the tribe Streptochaeteae, both species of the single genus, *Streptochaeta*, have been found to be diploids, with $2n = 22$. This count was reported for *S. sodiroana* (Pohl & Davidse, 1971) and *S. spicata* (Valencia, 1962).

We still do not have counts for two of the tribes of herbaceous genera: Anomochloeae of South America and Buergersiochloeae of New Guinea. We also lack counts for the majority of woody genera.

While the number of chromosomes in the set is important and further counts will be useful in understanding trends of evolution in the subfamily, karyotype analyses should also be undertaken. One such analysis was presented by Daker (1968), who investigated at Kew the cultivated material of the herbaceous bamboo, *Diandrolyra bicolor*. He found only 18 chromosomes in the set and his illustration shows that they are asymmetric. Another such analysis was made by Virkki (1963), who found 18 pairs of metacentric chromosomes in the bamboo, *Swallenochloa* (as *Chusquea*) *subtessellata*. In his study of *Streptochaeta spicata*, Valencia stated that of the eleven pairs of chromosomes he observed at metaphase, the position of the centromere was central in four pairs, while in the others the arms were slightly unequal.

Streptochaeta

A NEW SPECIES

One of the most unusual of the herbaceous bambusoid grasses is the genus *Streptochaeta*, whose remarkable "spikelet" has long been the basis of investigation and speculation. The genus was named by Schrader and published by Nees von Esenbeck, who examined the type specimen in the Berlin herbarium and published the name, *S. spicata*, in 1829. The type specimen came from Felisberto in the state of Bahia, Brazil. In his treatment of the bamboos of that country, Nees (1835) allocated the genera to three groups, one of which included *Streptochaeta* by itself. The following year he made it the basis of a tribe, Streptochaeteae (Nees, 1836).

The genus is found only in tropical America, with the most common species—the type—occurring from southern Mexico to northern Argentina. It is a medium-sized plant with broad, oval leaves generally 2–4.5 cm wide. A less widespread, but not uncommon, species is *S. sodiroana*, which ranges from Guatemala, Honduras, Belize, Costa Rica, and Panama to lowland Ecuador. It is a larger plant

with oval leaves that reach as much as 8 cm across and with smaller but more numerous spikelets in the inflorescence.

Until now, only two species have been known in the genus. However, a third can now be added. In 1972, during a collecting trip through eastern Brazil my colleague, Dimitri Sucre, and I located a population of *Streptochaeta* plants quite distinct from the known species. The genus was immediately recognized by the distinctive spikelets, although they differed from the known ones in size and other features. But the narrow, lanceolate blades presented an especially striking contrast to those of the other two species, which have among the broadest and most ovate blades of any grass. A study of the new species raised again the nature of the so-called "spikelet" in this genus, an interpretation of which I present in the discussion that follows its formal description. I am naming the new species, *Streptochaeta angustifolia*, in obvious reference to its distinctive blades.

Streptochaeta angustifolia Soderstrom, sp. nov. TYPE: Brazil, Espírito Santo, Mun. Cachoeiro de Itapemirim, 10 km from Cachoeiro toward Alegre, 20°47′S, 41°09′W, elev. ca. 90 m, *Soderstrom & Sucre 1969* (RB, holotype; CEPLAC, INPA, K, MO, P, US, isotypes).—FIGS. 5–6.

Gramen perenne, usque ad 70 cm altum. Laminae symmetricae, lanceolatae, 10–15 cm longae, 0.5–1.8 cm latae. Inflorescentia subspicata, 8–11 cm longa, 6–8 spiculis in spiram dispositis. Spiculae 1.0–1.5 cm longae, cum 11 bracteis spiraliter et verticillatim dispositis. Stamina 6, filamentis adnatis; antherae ca. 5.4 mm longae, apicaliter exsertae. Ovarium fusiforme, 3 stigmatibus, ca. 5 mm longis, non-plumosis, apicaliter exsertis.

Perennial with a knotty, short-rhizomatous base of sympodial habit. *Culms* unbranched, erect, hollow with thick walls, 40–70 cm tall, with 4–8 dark, prominent nodes, the internodes 4–14 cm long, in some instances many in succession shortened and resulting in a fascicle of leaves with the sheaths strongly overlapping. *Leaves* evenly distributed along the culm, acuminate at the tip, symmetric at the base, 10–15 cm long, 0.5–1.8 cm wide, scaberulous on the upper surface, glabrous or hirtellous on the lower, the margins entire, the midrib prominent on the upper and lower surfaces, the primary nerves 3 or 4 on each side of the midrib, manifest only on the lower surface, connected by manifest transverse veinlets. Sheaths strongly ribbed, pale green becoming brown, glabrous over the back, ciliate on the upper margins. Petiole lacking, the juncture of blade and sheath a smooth, dark band of tissue covered by cilia abaxially. *Inflorescence* terminating the culm with a second one occasionally produced from a bud in the axil of the uppermost leaf, 8–11 cm long, subspicate with 6–8 "spikelets" arranged spirally on the axis; peduncle 10–13 cm long, pale green, glabrous, becoming flocculose toward the summit, the axis flocculose, exserted well beyond its subtending leaf, the leaf blade sometimes reduced or lacking. *Spikelets* falling entire at maturity, 1.0–1.5 cm long with an awn 3–4 times as long; axis of the spikelet bearing numerous more or less spirally arranged bracts: bracts I–V greenish stramineous, membranous, short, empty, deeply dentate, I and II with 3 or 4 thick nerves, one extending into an awn, 1.3–3.6 mm long, positioned on the side of the spikelet toward the main axis of the inflorescence, near to each other but not overlapping; bracts III–V about the same size and shape, 4–5 mm long, with deeply dentate margins, and with 5 or 6 thick nerves, only slightly overlap-

FIGURE 5. *Streptochaeta angustifolia*.—a. Habit (×½).—b. Midregion of leaf showing summit of sheath and upper surface of blade (×4.5).—c. Midregion of leaf showing summit of sheath and lower surface of blade (×5).—d. Rhizome system with culm base (×1).—e. Portion of rachis enlarged (×1.5). [All drawings based on *Soderstrom & Sucre 1969*, Brazil, Espírito Santo, mun. Cachoeiro de Itapemirim.]

ping at the base; bract VI subtending a flowering axis and separated from bracts I–V by a curved glabrous internode, the bract ca. 1–1.4 cm long, elongate, coriaceous, lanceolate, concave, glabrous, 12-nerved, rounded on the back except for a flattened portion at the base from which extends a small, downward-pointing beak, narrowed above and forming a long, slender, tendrillike, coiled awn, 3–5 cm long; bracts VII and VIII lanceolate-triangular, the summits spreading away from each other, 8- or 9-nerved, the bases imbricate, coriaceous, 8.5–10.3 mm long; bract IX lacking; bracts X, XI, and XII a trimerous whorl embracing the androecium and gynoecium, convolute, coriaceous, 12–15-nerved, 12–14.5 mm long. *Stamens* 6, the filaments fused and forming a delicate tube around the gynoecium at anthesis, the anthers yellow, 5.4 mm long, exserted through the apex of the spikelet, the free part of the filaments above ca. 2 mm long, these attached to the anthers about ¼ from the base; ovary fusiform, ca. 4 mm long, the style to 3 mm long, the stigmas 3, nonplumose, ca. 5 mm long.

The inflorescence of *Streptochaeta*, including our new species, bears a number of short-pedicellate spikelets on an axis more or less spirally arranged. For *S. spicata*, Arber (1929) reported a 2/5 phyllotaxy and Page (1951) a 3/8 phyllotaxy. In that species there are 8–11 spikelets on the axis, in *S. sodiroana* up to 100, and in the new species, 6–8. In all of them the axis terminates in an aborted portion, sometimes represented only by a tuft of hairs.

The so-called spikelet (Fig. 6) of *Streptochaeta* is short-pedicellate and bears numerous bracts, again arranged around the axis in a more or less spiral to whorled, but not distichous, fashion. The first two are small and few-nerved, placed side by side, with margins free from one another, and facing the axis; these have thick nerves and are membranous between the nerves. The following three bracts are of the same consistency with thick nerves, deeply dentate margins, but are a little larger than the first two; they are somewhat overlapping at the base. The sixth and succeeding bracts are coriaceous, elongate, many-nerved, and curved. Bract VI bears a long coiled and twisted terminal awn. At maturity the awns of the spikelets become entangled and all the spikelets usually fall or are carried away together.

Above bract VI are two elongate bracts with overlapping bases and narrowed summits that are falcate and point away from each other. Above this pair are three more elongate and coriaceous bracts that form a whorl around the reproductive organs; their margins are overlapping at the base. All of these bracts, the sixth and succeeding ones, form essentially a hard, more or less tubular, structure that surrounds the reproductive organs.

The androecium is composed of six stamens whose filaments are fused at the base. At anthesis the tube elongates and the anthers are thrust out through the top of the spikelet, with the extremely thin, delicate, and transparent tube surrounding the ovary. The anthers are attached to the filaments about one-quarter from the base and do not hang from the spikelet in a versatile manner. The

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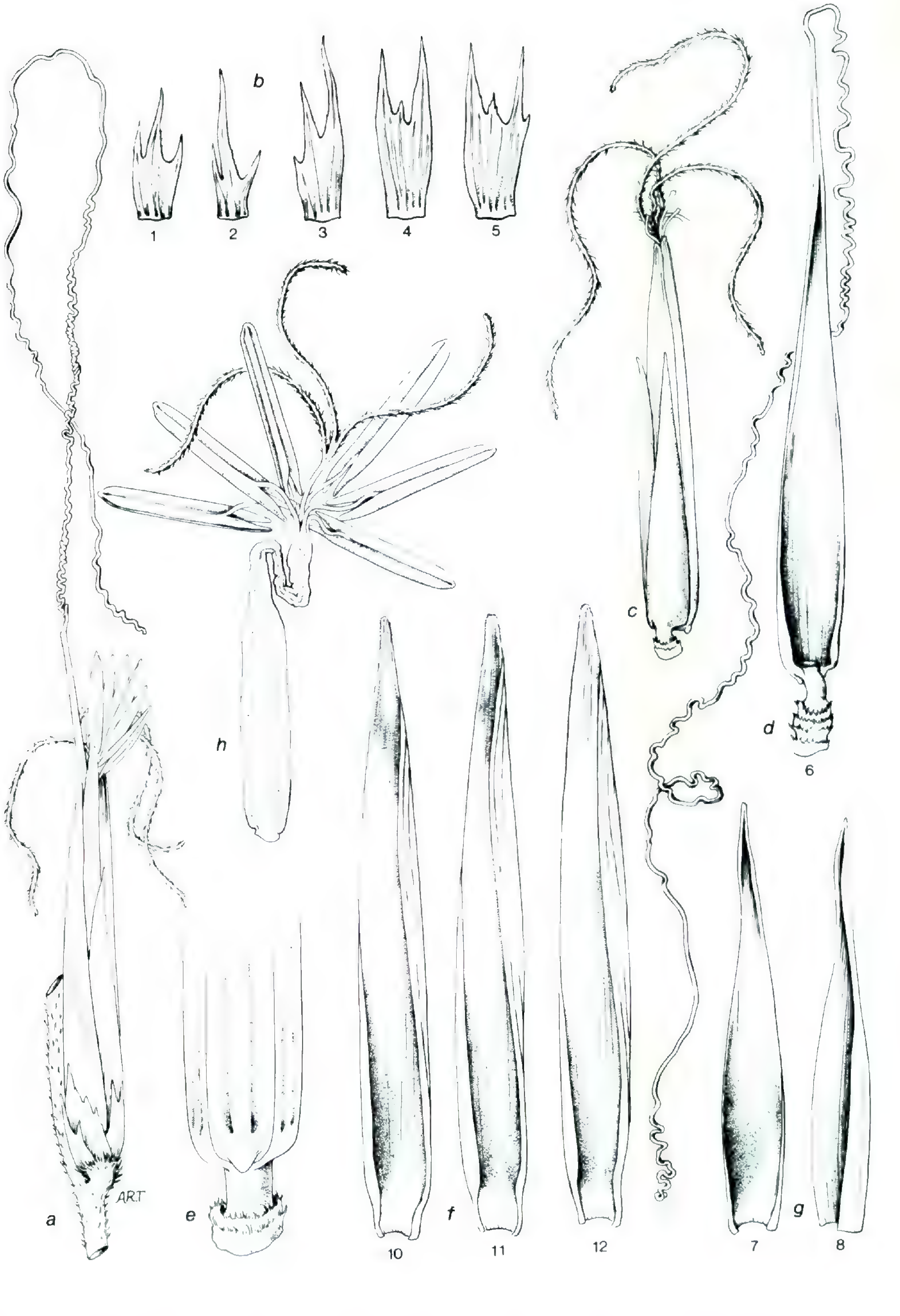
FIGURE 6. *Streptochaeta angustifolia*.—a. Pseudospikelet (×4.5).—b. Series of bracts (1–5) from the base of the pseudospikelet (×6).—c. Pseudospikelet with basal bracts 1–5 removed and showing bracts 7 and 8, whose bases are overlapping (×4.5).—d. Bract 6 with long coiled awn (×4.5).—e. Back portion of the base of bract 6 showing region where embryo exits at germination.—f. Bracts 10–12 (×6).—g. Bracts 7 and 8 (×6). Bract 9, which exists in other species, has not been found here.—h.



Ovary with long style and 3 stigmas, surrounded by the thin, fused filaments of the 6 stamens (×4.5). [All drawings based on *Soderstrom & Sucre 1969*, Brazil, Espírito Santo, Mun. Cachoeiro de Itapemirim.]

gynoecium consists of an elongate ovary, a long style, and three long, nonplumose stigmas that also exit through the summit of the spikelet.

After fertilization the ovary develops into a fruit with a long, linear hilum and small embryo. It is tightly enclosed within the hard bracts, all of which remain together as a unit through germination. At germination the embryo pushes through the noncoriaceous bases of the upper bracts and through a special tissue at the base of bract VI.

ANALYSIS OF *STREPTOCHAETA* SPIKELET

Several important anatomical and morphological studies have been carried out on the genus, the most significant being those of Arber (1929, 1934), Metcalfe (1960), and Page (1947, 1951). The anatomical findings of Page and Metcalfe showed that the leaf is of the bambusoid type, with its complex system of vascular bundles in the keel, the nonradiate chlorenchyma made up of arm cells, and the presence of fusoid cells. The epidermis is also of the bambusoid type, and so is the seedling, as I have shown. Furthermore, the chromosome number of $2n = 22$ corresponds to that of other herbaceous bambusoid grasses of the New World, especially members of the tribes Olyreae and Parianeae. These New World bambusoid grasses, based on numbers derived from $x = 12$, have highly evolved and often specialized inflorescences, a pattern shared by *Streptochaeta*. There is no reason to concur with Butzin (1965), who made this genus the basis of a monotypic subfamily.

The nondistichous arrangement of the spikelets on the inflorescence axis and similar arrangement of the multiple bracts on the spikelet axis have confused botanists since the day the genus was described. The genus has been the subject of investigation by numerous morphologists, and many papers have been published with widely divergent hypotheses concerning the interpretation of the spikelet, among these the works of Doell (1880), Čelakovský (1889), Hackel (1890), Arber (1929), and Page (1951). All authors have agreed that *Streptochaeta* is a primitive grass, perhaps the most so in the family.

Until now interpretations of the spikelet of *Streptochaeta* have been overly influenced, in my opinion, by the nondistichous arrangement of its many parts, in a family where distichy is the rule. Twisting and torsion are prevalent in this taxon, however, and one can see the twisted inflorescence axis with the naked eye. Such a twisting could camouflage a distichous arrangement and bring the parts into a somewhat spiral phyllotaxy. This twisting was probably repeated in the axis of the spikelet, at least historically, and this, with shortening of internodes, could account for some parts appearing to be in whorls. Within the Bambusoideae nondistichous placement of parts is not altogether unusual; as examples, I refer to the glumes of the male spikelets of *Pariana* placed side by side and to the spiral arrangement of spikelet bracts (glumes) in the inflorescence of the bamboo, *Melocanna*, as reported by Petrova (1973). The nonbambusoid grass, *Micraira*, is well known for the spiral arrangement of its leaves.

Page (1951) found that buds would sometimes form in the axils of bracts I–V in *S. spicata*, and Arber (1929) encountered them in some bracts in *S. sodiroana*. While such buds do not normally develop further, even when present, Page found

that in rare instances the bud subtended by bract V would develop partially. In such a case the bract itself elongated, became coriaceous, and produced a coiled awn just like that of bract VI, to which it may thus be considered homologous. Bracts I–VI are therefore homologous structures.

Except for their nondistichous placement on the axis, then, we can consider bracts I–V to be homologous structures that are potentially gemmiferous and are homologous to bract VI, which is long, coriaceous, many-nerved, long-awned and sometimes interpreted as the fertile lemma. It subtends further structures that precede the reproductive organs. These further structures include a pair (sometimes a third developing) with the bases overlapping, sometimes interpreted as two halves of a palea, followed by a whorl of three, universally interpreted as lodicules.

There is no problem in the interpretation of the reproductive organs themselves. The gynoecium bears three, long nonplumose stigmas. Three stigmas are commonly found in bamboos, such as *Arundinaria* and *Bambusa*, and nonplumose stigmas are to be found in such genera as *Eremitis*, *Anomochloa*, *Streptogyna*, and *Pharus*. The androecium consists of six stamens whose filaments are fused at the base and at anthesis extend into a thin, delicate, and translucent tube that surrounds the ovary. Six stamens are of frequent occurrence in the Bambusoideae and are to be found in such genera as *Bambusa* and *Elytrostachys* of the New World and *Melocanna* of the Old. The anthers are thrust through the opening at the top of the spikelet as are the stigmas. They are attached about one-quarter from the base and do not hang in a versatile manner as the anthers of many wind-pollinated grasses. The staminal tube formed by the filaments is extremely thin and fragile, a condition that could only occur in a closed and protected environment, such as that afforded by the whorl of three coriaceous structures that completely envelop and protect it.

The fusion of filaments into a staminal tube occurs throughout the Bambusoideae, and to my knowledge six stamens are always involved. We find this in the herbaceous bambusoid genus, *Froesiochloa*, as well as in all or some species of the following bamboos: *Dendrocalamus*, *Gigantochloa*, *Oxytenanthera*, and *Schizostachyum*. In all of these cases the anthers exit through the apex of the spikelet and the tube is enclosed within hardened scales.

Thus, stamens of *Streptochaeta* are unlike those of most grasses in that the anthers are thrust through the top of the spikelet rather than laterally from it where they can hang in a versatile condition. Whatever the mechanism of pollination may be in this genus, the position of the anthers and the nonplumose nature of the stigmas speak against wind as the agent of pollen transfer, a situation not unknown in the subfamily (Soderstrom & Calderón, 1971).

In most grasses that are wind-pollinated, the bracts (usually lemma and palea) that embrace the reproductive organs spread apart and allow the stamens and stigmas to extend laterally, and after fertilization they again close and protect the developing fruit. The pushing apart of the lemma and palea is brought about by the lodicules which at this moment become swollen and turgid, thus forcing apart these structures. After fertilization they become flaccid and the lemma and palea come together again.

Dobrotvorskaya (1962), who has made extensive studies on lodicules, consid-

ers this to be their primary function. She also feels that they play a role in protecting the ovary and regulating its water metabolism.

In *Streptochaeta* the anthers do not exit laterally, which we can simply observe or deduce from the fused filaments, a condition that would not allow this. The nonplumose stigmas also corroborate the fact that we are not dealing with a wind-pollinated grass in which laterally exiting, versatile anthers are the rule. The primary function of lodicules in *Streptochaeta*, then, does not exist.

In other bambusoid grasses where there is a staminal tube and the anthers exit terminally, there are no lodicules. In all species of *Gigantochloa* the filaments form a tube and lodicules are lacking. I have not found lodicules in *Froesiochloa*; and in those species of *Schizostachyum* that have a staminal tube there are none. In other cases, where the filaments are free but are enclosed in hard scales that do not open and the anthers exit terminally, the lodicules are likewise absent. Such is the case in *Anomochloa* and *Bambusa atra*.

It seems reasonable to assume that *Streptochaeta* has followed the same course of evolution as other bambusoid grasses, and so with the development of the staminal tube and terminal exiting of the anthers there would also be loss of lodicule function and therefore loss of the lodicules themselves. Furthermore, the structures that have been called lodicules are so unlike these organs in any grass, bambusoid or otherwise, that it is difficult to accept them as such. Rather, they may be bracts that are homologous to the "palea bracts," which in turn are homologous to bracts I–VI.

Dobrotvorskaya (1962) presented data from her study of these "lodicules" in *Streptochaeta* that corroborates this hypothesis, even though she did not question their true nature. She referred to the genus as the most primitive grass and accepted the three large scales as lodicules. She pointed out that they protected the delicate staminal tube and resembled bracts to a great degree, not corresponding to usual lodicules, which are small scales. Dobrotvorskaya found that the cells in the lower part of the *Streptochaeta* lodicules reached gigantic size and she compared these to similar cells found in the inner epidermis of the lemma and palea of grasses in the tribe Hordeae. She also observed similar large cells in the lemma and palea of *Anthoxanthum odoratum*, an especially interesting observation, for in that species the ovary is enclosed in a hardened lemma and palea and lodicules are lacking. Thus, the anatomical evidence presented by Dobrotvorskaya favors the interpretation that the lodicules of *Streptochaeta* are bracts homologous to lemmas (or lemma and palea) that protect the ovary, have a water-storage function, and perform a role in the process of floral development.

At this point we should refer to teratological specimens that were studied by Page (1951). She found that in cases where the bud of bract V developed, the bract itself elongated and became similar to bract VI, complete with a long, coiled awn. At the same time the following two bracts, VII and VIII, elongated and produced small, coiled awns, thus indicating an homology between these bracts and all of the preceding ones. Page also presented evidence to show that bracts VII and VIII were on a different axis from bracts I–VI.

A further important point is that in the early stages of development a ridge always develops opposite and above bracts VII and VIII. On rare occasions, in *S. spicata*, Page (1951) found that the ridge developed into a full-grown bract and

completed a whorl of three. Some authors, such as Arber (1929), argued that bracts VII and VIII represented halves of a palea, and the interpretation of these two as members of an outer perianth was the basis of Čelakovský's theory in 1889 that the grass palea originated from two outer perianth parts. Page, however, showed that all three had separate origins, a fact that thus negated these hypotheses.

If the three large bracts that surround the reproductive organs are not lodicules and the two (or three) below them are not halves of a palea, what do they represent? By their size, many-nerved condition, and coriaceous nature, they most resemble bract VI, except for the coiled awn, and I have already pointed out that the "palea bracts" sometimes do, in fact, develop coiled awns that indicate homology with bract VI. I have already suggested that the whorled arrangement of bracts may be brought about by twisting of the axis and shortening of internodes, conditions that appear to be the rule in the inflorescence of this genus.

THE PSEUDOSPIKELET OF BAMBOOS

Two items are especially pertinent to my interpretation of the *Streptochaeta* spikelet: (1) bracts I–V are potentially gemmiferous, and (2) the genus is a member of the Bambusoideae. On the first point rests the assumption that we are not dealing with a spikelet but an inflorescence branch, and on the second the opinion that we should interpret such a branch by analogy to similar structures within related bambusoid grasses.

The numerous, potentially gemmiferous, bracts that we find in the spikelet of *Streptochaeta*, represent a condition that is common in bamboos. Kurz (1876: 262) was, to my knowledge, the first to draw attention to the structure, but it was McClure (1934) who analyzed it in some Chinese species of *Schizostachyum*, and gave further definition to it in later works (1966, 1973). As defined by McClure, a pseudospikelet is a spikeletlike branch of an indeterminately branching inflorescence, and I interpret this to be the condition that we encounter in *Streptochaeta*. I shall henceforth use the term pseudospikelet for the flowering unit in this genus and interpret it by analogy to the pseudospikelet that characterizes many bamboos, rather than to the spikelet that characterizes most other grasses.

As an example of the pseudospikelet, I have illustrated the inflorescence of *Bambusa atra* (Figs. 7a–b), a bamboo native to the Moluccas. As is typical of plants with pseudospikelets, the leaves of the branch, prior to flowering, become progressively smaller until they are represented by sheaths only, each small sheath subtending a bud that may grow into a short flowering axis that is like a spikelet in appearance. While this axis terminates in a spikelet, with bracts (lemmas) that subtend flowers, there are additional bracts below this that subtend prophyllate branch buds instead of being empty like usual glumes. Such a primary pseudospikelet is diagrammed in Fig. 8d. Here the whole axis is subtended by a bract and bears a prophyllum at its first node. A structure comparable to the ordinary spikelet consists of the upper bracts that subtend floral axes (palea and flower) and two empty bracts (glumes) below this series. Below these empty bracts occur several more bracts like the empty ones in all ways except that each subtends a prophyllate bud. This primary pseudospikelet, as shown in Fig. 8c,

FIGURE 7. *Bambusa atra*.—a. Young inflorescence branch (×½).—b. Mature inflorescence branch (×½).—c. Leaf complement (×½).—d. Upper portion of culm leaf from inside to show ligule (×¼).—e. Upper portion of culm leaf from outside (×¼).—f. Culm leaf in place (×¼).—g. Ligule and auricle of foliage leaf (×3). [All drawings based on fresh material of *Soderstrom & Kulatunge 1600* from plant cultivated at Peradeniya, Ceylon.]

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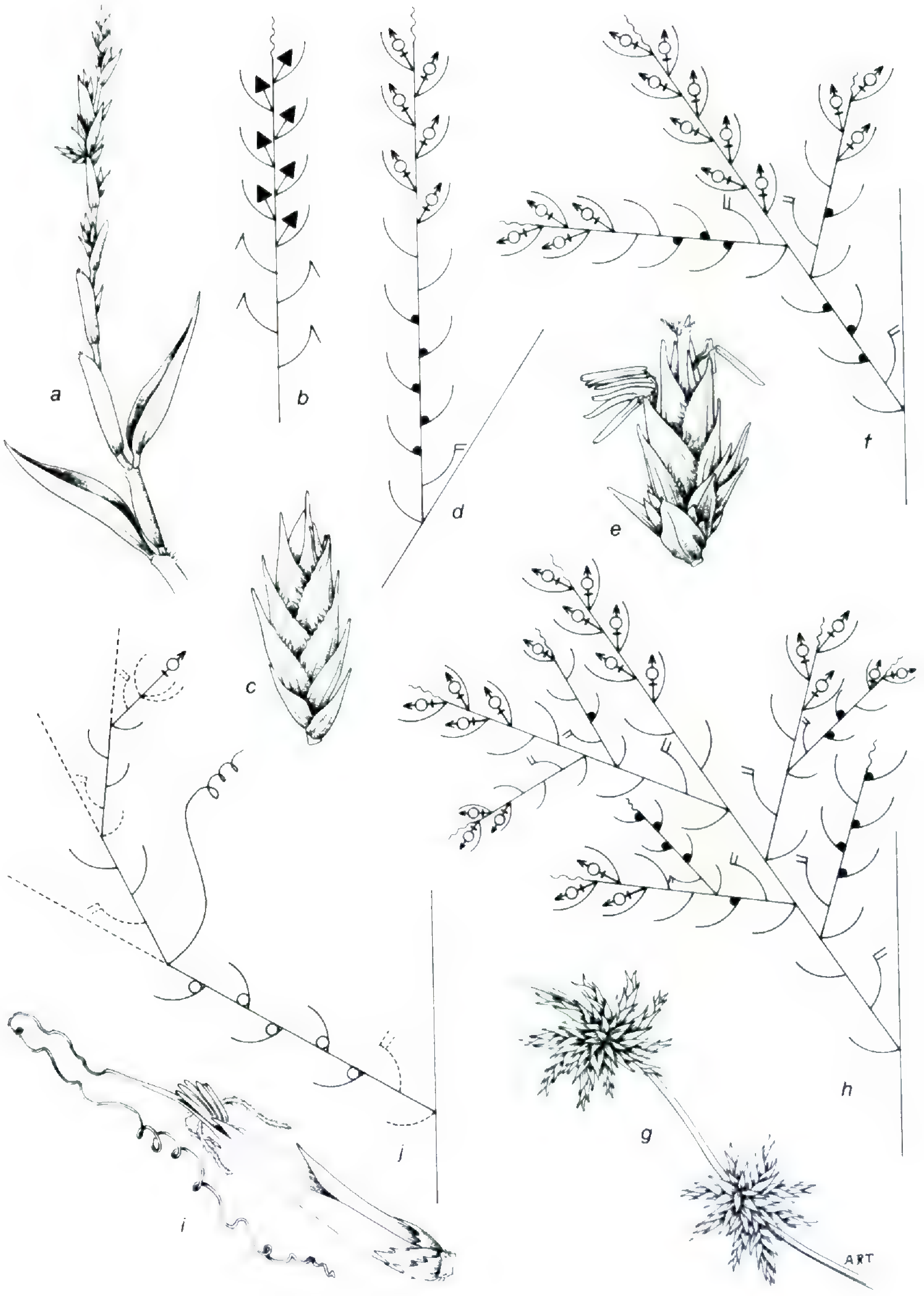
FIGURE 8. Flowering systems of *Bambusa atra* and *Streptochaeta angustifolia*.—a. Flowering branch of *Bambusa atra*.—b. Schematic diagram of a.—c. Primary pseudospikelet of *Bambusa atra*.—d. Schematic diagram of a primary pseudospikelet such as c.—e. Primary pseudospikelet of



Bambusa atra with secondary pseudospikelets developing in the axils of the basal bracts.—f. Schematic diagram of a primary pseudospikelet with early secondary pseudospikelets, such as e.—g. Mature clusters of pseudospikelets of *Bambusa atra*.—h. Schematic diagram of a fully mature pseudospikelet cluster such as g.—i. Representation of pseudospikelet of *Streptochaeta angustifolia*.—j. Schematic and interpretative diagram of the pseudospikelet in i. [Solid triangle indicates a primary pseudospikelet; open circle with male and female signs indicates fertile floret; solid circle indicates a bud; double-barred flag represents a prophyllum; curved line with hanging tip represents leaf sheath and blade, respectively; curved line alone represents a sheath or subtending bract; broken line represents hypothetical missing structure; wiggly line represents terminal aborted part of axis.]

looks like an ordinary, many-flowered spikelet, but its indeterminate nature becomes apparent upon germination of the lower buds, which themselves develop into flowering axes, or secondary pseudospikelets, as shown in Fig. 8e and diagrammed in Fig. 8f. These secondary pseudospikelets themselves can produce further, tertiary, pseudospikelets, the final result being a cluster of spikelets of various orders, as shown in Fig. 8g and diagrammed in Fig. 8h.

In the case of *Bambusa atra*, which is represented in Fig. 8, the primary pseudospikelets are, of course, the first to develop, but within each spikelet maturation of the florets proceeds acropetally, with the uppermost ones remaining incomplete or aborted.

The number of bracts on a floral axis and the number that are empty or that subtend buds (floral or branch) are variable, as is the quantity of pseudospikelets ultimately produced. In some species (such as *Bambusa glaucescens*) only a few secondary pseudospikelets develop, while in others many are formed in each order and result in a large and dense sphere (as in species of *Dendrocalamus* and *Oxytenanthera*).

Subtending bracts and prophylla in the inflorescence are common in bamboos that bear pseudospikelets. The development of the usual spikelet of determinate growth very likely came about by the loss of subtending bracts, prophylla, and some of the buds. Without much imagination we can derive the spicate inflorescence of *Streptogyna* from a theoretical type like that shown in Fig. 8b by loss of the subtending bracts and in each floral axis loss of the prophyllum, loss of the prophyllate buds in the lower bracts (glumes), and the retention of flowering buds in the upper ones (lemmas). In some cases, such as the bamboo *Chusquea*, four empty bracts generally precede the fertile one (lemma), which subtends a flower. McClure (1973) has referred to these empty bracts as "transitional glumes" to distinguish them from "glumes," which in the ordinary spikelet means the two empty bracts that precede the lemma(s).

The grass panicle can be derived from an elongation of each flowering axis, as shown in Fig. 8h, loss of subtending bracts and prophylla, and of buds from the lower bracts. This would result in determinate spikelets with empty glumes and fertile florets, each pedicellate, and arranged in a panicle, which is common to most grasses.

THE PSEUDOSPIKELET OF *STREPTOCHAETA*

If we regard the flowering unit of *Streptochaeta* as a pseudospikelet and accept the parts as spirally or verticillately arranged due to variations in twisting of the axes and telescoping of the internodes, we can compare it to a fully developed pseudospikelet, as found in *Bambusa atra* (Figs. 7b, 8a–h). Such a comparison allows the following interpretation (cf. Figs. 8i–j):

Bracts I–VI are arranged on the axis (2) of the primary pseudospikelet which aborts at the tip, repeating abortion of the apex of the main inflorescence axis (1). The bract that theoretically would subtend the axis (2) and the prophyllum of this axis have been lost through evolution. The bud subtended by bract VI always germinates and produces a new axis (3), which, theoretically, is the axis of a secondary pseudospikelet. Bract VI is the first of the several coriaceous bracts that surround the reproductive parts and its long, coiled awn later assists

in the dispersal of the fruit that it ultimately harbors. (At this point it is interesting to recall that when the bud subtended by bract V develops, that bract takes on a form and function like bract VI.) Page has given evidence to show that bracts VII and VIII (and therefore IX, which follows) are on an axis separate from bracts X–XII, so I have diagrammed them (Fig. 8j) as on another axis (4), and assumed that the tip of this axis aborted through evolution and that its prophyllum has likewise been lost. Assuming that the branching pattern repeats itself, bract IX theoretically subtends axis (4); this subtending bract sometimes develops. Axis (4), which belongs to the tertiary pseudospikelet, bears three bracts, X–XII, which previous investigators have considered to be lodicules. This axis conceivably could terminate in the flower but if we assume the branching pattern to be consistent throughout, we must assume that the tip of axis (4) aborted in the course of evolution and that bract XII subtends the floral axis. This axis is surrounded and protected by bracts X–XII and the prophyllum (palea) has been lost through evolution as well as the lodicules. The absence of lodicules, androecium of 6 stamens, and gynoecium with 3 stigmas corresponds to the condition we find in *Bambusa atra,* with which we have compared the pseudospikelet of *Streptochaeta.*

When we reexamine bracts I–XII, it becomes apparent that there are three sets of different kinds of bracts. Bracts I–VI are small and scalelike except when subtending a bud that germinates, as is always the case with bract VI and occasionally with bract V. The next set of bracts are VII and VIII, with IX sometimes developed; these two or three are long, coriaceous and many-nerved with falcate tips. Bracts X–XII are also long, coriaceous, many-nerved, and with long, but erect, acute tips. Each set of bracts, similar among themselves but with some differences between each other, pertains to a separate axis: bracts I–VI to the axis of the primary pseudospikelet, VII–IX to that of the secondary pseudospikelet, and X–XII to that of a tertiary pseudospikelet. What has commonly been referred to as the spikelet in *Streptochaeta* is thus a highly modified branching system made up of three orders of pseudospikelets.

Streptochaeta is the only herbaceous bambusoid grass that has retained the pseudospikelet, with the possible exception of *Anomochloa* and the African genera, which I have not yet studied. But like other herbaceous bambusoid grasses its inflorescence has become highly specialized, resulting in a greatly telescoped and modified branching system. I would agree with previous investigators that *Streptochaeta* is among the most primitive of grasses. However, I base this opinion not on its possession of three lodicules and a two-parted palea, structures that I reason are not even present, but on its herbaceous nature and retention of a pseudospikelet.

The Primitive Bambusoid Grass

The major natural groups of grasses as we recognize them today (e.g., arundinoid, pooid, oryzoid, bambusoid) doubtless became differentiated early in the evolution of the family and derived from a form adapted for wind pollination. Various extant grasses possess certain features that we presume to be primitive in that they are common to the larger group, monocotyledons, to which grasses belong. We assume that these features, such as three (possibly six) lodicules or

perianth parts, six stamens, and three stigmas, were present in the primitive form that preceded all the major groups.

Chromosome numbers in multiples of six are characteristic of many grasses, including *Oryza* and *Luziola* of the Oryzoideae, *Centosteca* and *Lophatherum* of the centostecoid group, *Arundo* of the Arundinoideae, and many genera of the Bambusoideae. We may postulate that six is indeed the basic number in the subfamily Bambusoideae, although no count of $2n = 12$ has ever been recorded.

To my knowledge, none of the original bambusoid grasses that were diploids of $2n = 12$ now exists. Probably $x = 12$ occurred long ago through doubling and thus brought about this new basic number of polyploid origin. Stebbins (1971: 190–191) pointed out that in "old, mature, or declining polyploid complexes certain segments initiate new series of polyploid numbers in which the basic number that is multiplied is not the original basic number of the complex [in our case, $x = 6$] but some multiple of it [$x = 12$]." These new series are called "secondary cycles of polyploidy."

At the original tetraploid level of $2n = 24$, there was a period of diversification and differentiation before the higher polyploids appeared. Herbaceous genera such as *Streptogyna*, *Pharus*, *Leptaspis*, and *Puelia* may represent original tetraploids that were adapted to forest conditions. While most such genera have since become extinct, these few—particularly the first three—may have survived because of their adaptation to more disturbed forest conditions than the rest and a more widespread distribution made possible by excellent dispersal mechanisms.

Among the Bambusoideae we consider the above genera, with $2n = 24$, to be diploids, based on the basic number of 12 as opposed to the theoretical basic number of 6. The primitive grass leaf probably had an anatomy most like the present-day pooid type, with a relatively undifferentiated mesophyll and simple epidermis lacking bicellular microhairs. The various modifications that took place in the bambusoid leaf, such as the development of arm cells and fusoid cells, may have been derived from that as an adaptation to the shaded, humid forest conditions which characterize the habitat of the herbaceous bambusoid genera.

Bamboos, whose leaf anatomy and epidermis differ little from those of the herbaceous members, must have evolved from herbaceous ancestors. Bamboos are mostly polyploids, based on $x = 12$, usually tetraploids but in some cases hexaploids. Development of the large woody habit may have been in response to competition with the tree, the major growth form of the forest. The process that led from herbaceous to woody involved an increase in the chromosome number, or polyploidy, development of complex branching at the nodes, an overall increase in size, and emphasis on vegetative growth, such as the development of a strong rhizome system.

This particular stress on vegetative growth with greater longevity of the individual culm and increase in size by branching in the bamboos led, at the same time, to a decrease in flowering. Vegetative reproduction became the dominant condition in bamboos, at the expense of sexual reproduction, which now occurred only at intervals, these sometimes as long as 120 years. With flowering so infrequent, the simultaneous occurrence of this event in two species became too remote a possibility for gene exchange between them to play part in further evolution. By their diminished flowering and the loss of active inflorescence evolution, the bamboos became in essence guardians of ancient flowering systems,

long since lost in all other grasses—including the herbaceous bamboos—that flower every year.

We find such a primitive type of inflorescence in bamboo genera like *Bambusa, Dendrocalamus,* and *Oxytenanthera,* where the leaves of a vegetative branch become progressively smaller until they consist only of sheaths that subtend reproductive buds. These buds develop into indeterminate spikeletlike branches called "pseudospikelets." In the most primitive form, such as in *Bambusa,* the flowers in these pseudospikelets are complete, with three well-developed lodicules, six stamens, and three stigmas. From such a pseudospikelet with complete flowers, we can follow the hypothetical evolution of the usual grass spikelet and its arrangement in a "raceme" or "panicle." Such a development must have come about by the loss of subtending bracts, prophylla, and buds, which are common in the pseudospikelet, and a decrease in the number of all parts of the flower.

We would predict that in the most primitive herbaceous bambusoid grass the leaves of the axis, as in *Bambusa,* would become progressively smaller until they were reduced to sheaths that subtend pseudospikelets. Except for the lack of subtending bracts, the closest we come to this is *Streptochaeta,* where the pseudospikelet is highly modified. The inflorescence of *Streptogyna* is also primitive in its spicate arrangement, although subtending bracts are not present and the spikelets are of the usual determinate type. In both of these genera, however, the spikelets are bisexual, the former with an unspecialized androecium of six stamens and gynoecium of three stigmas, and the latter with an advanced androecium of three stamens and gynoecium sometimes of two stigmas. The inflorescence of *Anomochloa* may be unspecialized and certainly begs analysis; however, the flower is highly specialized in its lack of lodicules, four stamens, and single nonplumose stigma. The many-flowered, bisexual spikelets of the African genera, *Puelia* and *Guaduella,* which are arranged in panicles, also need further study.

The most highly evolved inflorescences of herbaceous bambusoid grasses are those that are monoecious with one-flowered spikelets. Four tribes exhibit this condition: Buergersiochloeae, Olyreae, Parianeae, and Phareae. Although Raven & Axelrod (1974: 594) speak of the olyroid grasses as relatively unspecialized, they are, on the contrary, the most specialized in the subfamily. Genera of this tribe have not only reached the monoecious state but within the same plant there is often great differentiation between male and female inflorescences. The tribe, with variable chromosome complements derived from basic numbers lower than 12, appears to be in a state of active evolution. The only herbaceous bambusoid grasses that are diploids based on $x = 12$ are found in the tribes Phareae, Streptogyneae, and Atractocarpeae. All of these tribes are also present in Africa: the first contains *Pharus* of the New World and *Leptaspis* of Africa and Asia; the second contains the genus *Streptogyna* with one species in the New World and one in Africa and Asia; and the third contains two genera—*Guaduella* and *Puelia*—endemic to tropical West Africa. Interestingly, the leaf epidermis of all of these lacks bicellular microhairs, which are commonly found in bambusoid grasses. The seedlings of those studied—*Pharus* and *Streptogyna*—do not have reduced leaves and are the most unspecialized in the subfamily.

We do not, then, have a single most primitive bambusoid grass but rather several, each possessing certain primitive features. The most unspecialized inflo-

rescences of pseudospikelets are found in the polyploid woody genera like *Bambusa*, while the primitive herbaceous growth form occurs in diploid genera like *Streptogyna*. Both of these have chromosome complements based on the primitive basic number of 12.

Streptochaeta, long regarded as the most primitive grass, cannot hold this title alone. It may indeed be regarded as primitive in its herbaceous condition, modified pseudospikelet, and flower that contains six stamens and three stigmas. But its lack of lodicules, nonplumose stigmas, seedlings with reduced leaves, and a chromosome complement based on a derived basic number of $x = 11$, all show advancement.

I do not yet have enough information to postulate the origin of bamboos, but I feel that they have developed from herbaceous stock and have a close and common ancestry. The genera are still not well understood and valid phytogeographical comparisons cannot yet be made. We do know, however, that Africa is poor in bamboos, with few genera and species represented, while Madagascar is the home of several distinct genera. The chromosome numbers of American bamboos tend to be lower while those of Asia are higher, with the greatest concentration of hexaploids occurring in northern Burma and western China.

Clearly we must now study the herbaceous bambusoid grasses of tropical West Africa and the bamboos that occur on Madagascar. An understanding of these may offer further clues regarding the earliest development of the subfamily and aid us in our interpretation of its evolution.

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EVOLUTION OF REPRODUCTIVE SYSTEMS IN THE GRAMINEAE[1]

H. E. Connor[2]

ABSTRACT

From a simple hermaphrodite flower, and from a complex incompatibility system unique among the flowering plants, several breeding systems have evolved in the Gramineae. Self-compatibility is the most commonplace variant and following this mutation, habitual or facultative cleistogamy is a simple evolutionary step. Separation of the sexes to different plants as in dioecism is relatively uncommon (ca. 20 genera), and gynodioecism is much less frequent still (3–4 genera). Both are seen as escape pathways from self-compatibility; the development of such pathways is discussed. Separation of the sexes to separate flowers as in monoecism is relatively common and with the variants andromonoecism and gynomonoecism is the most substantial departure from hermaphroditism in the family. These states are also interpreted as responses to self-compatibility; and though they do not generate cross-fertilization, they assist its evolution. Pathways for the evolution of these breeding systems are described. Apomixis and the breeding system best suited are discussed.

Reproductive biology in the Gramineae begins at the transition in the shoot apex from leaf production to the initiation of inflorescence primordia and the later development of floral structures. These have been well described for numerous grasses (Barnard, 1955, 1957, 1964; Bonnett, 1966; Sharman, 1960), and are mediated by photoperiod. The review of Evans (1964) elegantly reveals data on the interplay of daylength, temperature, and vernalization on inflorescence development.

Floral induction and initiation may occur in the season of flowering (Evans, 1964), or in the season preceding inflorescence emergence (Mark, 1965; Hodgson, 1966). Inflorescence emergence is temperature or daylength dependent (Cooper, 1952; Connor, 1963; Heslop-Harrison, 1961). Temperature also controls anthesis, and later the release of pollen from anthers.

Photoperiod, however, has other effects on the reproductive cycle. It may, for example, affect the frequency of cleistogamy in facultatively cleistogamous grasses (Langer & Wilson, 1965), or in a facultative apomict the frequency of apomictic or sexual embryo sacs (Knox, 1967; Knox & Heslop-Harrison, 1966), or depress maleness (Heslop-Harrison, 1959), or reduce the number of florets in the male inflorescence of *Zea mays* (Moss & Heslop-Harrison, 1968), or control protandry and protogyny (Emerson, 1924).

Although these environmental influences are considerable, genetic influences may cause transient male and female sterility, or restore lost fertility in part or in whole, or promote redistribution of the sex-forms. A combination of both genetic and physiological factors may introduce difficulties into an interpretation of the breeding system of any grass.

At the International Symposium on Reproduction in Flowering Plants held at Christchurch, New Zealand, in 1979, I presented a survey of the breeding systems known in the Gramineae (Connor, 1980). This present paper is complementary

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to that; the bibliographies of both papers supplement each other. Here, as there, I follow the organization of tribes proposed by Hubbard (1973) for the grasses.

The Flower, the Spikelet, and the Inflorescence

The primitive grass flower is postulated as having three bracts and lodicules, six stamens, and a 1- or 3-locular tristigmatic gynoecium (Schuster, 1910; Arber, 1934; Clifford, 1961). The spikelet is considered to have been many flowered, and the inflorescence is thought to have comprised many of these spikelets in a simple more- or less-branched, terminal panicle. Associated with these characteristics is the further postulate of entomophily (Schuster, 1910; Clifford, 1961; Stebbins, 1956, 1974).

From these very reasonable postulates there is a general evolution in the flower by reduction to two bracts and lodicules, three stamens, two stigmas and one ovule, though this combination is by no means universal. Associated features that are interpreted as part of an anemophilous syndrome are: rapidly elongating staminal filaments; easily exserted stigmata; readily dispersed pollen; a single ovule per flower; and the preservation of a self-incompatibility system.

Within the flower some further reductions are detectable, e.g., lodicules may be lacking or be so small as to be ineffective. Absence of lodicules is frequently associated with protogyny in hermaphrodite flowers but may also occur in monoecious and dioecious taxa; see summary in Connor (1980). Stamens may be reduced to two or one per flower; this state seems randomly distributed among the tribes and is independent of what seems its logical correlative—cleistogamy (Connor, 1980).

Among spikelets there are some trends in common. Geminate dimorphic spikelets of the form one sessile and the other pedicelled may be found in such different tribes as the Phareae and Olyreae (Bambusoideae) and in the Andropogoneae and Maydeae (Panicoideae). This form is frequently associated with a discrimination such that male elements alone are in pedicelled spikelets and female organs in sessile ones. A single hermaphrodite floret borne terminally in a spikelet of two or more florets may be found in the Bambuseae, Arundinelleae, Aveneae, Paniceae, and Andropogoneae. The ultimate reduction is to one floret per spikelet, and this is found in such differing tribes as Phareae, Agrostideae, and Sporoboleae.

The precise evolutionary phases displayed in inflorescence development are not topics for this paper except as they display relationships to sex-form. Among monoecious genera there is a slight trend towards axillary female inflorescences and terminal male inflorescences, e.g., *Humbertochloa, Hydrochloa, Luziola,* and *Zea*. Axillary inflorescences are a feature of some herbaceous members of the Bambusoideae; in such genera as *Arberella, Raddia,* and *Strephium* they occur at almost all the nodes, but in *Olyra* axillary branches occur at uppermost nodes only (Calderón & Soderstrom, 1973; Soderstrom & Calderón, 1979a). These genera are also monoecious but the axillary inflorescences are of mixed male and female spikelets.

Clayton (1969) detects in the Andropogoneae an evolution towards numerous smaller axillary inflorescences along with the development of the spathe and the

TABLE 1. Reproductive systems in the tribes of grasses; + = present.

Tribe	Hermaphroditism	Monoecism[a]	Dioecism[b]	Apomixis	Cleistogamy
Arundineae	+	+	+	+	
Chlorideae	+	+	+	+	+
Eragrostideae	+	+	+	+	+
Festuceae	+	+[c]	+[c]	+[c]	+
Paniceae	+	+	+	+	+
Andropogoneae	+	+		+	+
Aveneae	+	+		+	
Hordeeae	+	+		+	+
Pappophoreae	+	+	+		+

[a] Including andro- and gynomonoecism.
[b] Including gynodioecism.
[c] Mostly contributed by *Poa*.

spatheole; these form false panicles and it is supposed that they developed from an apparently primitive terminal panicle.

As a whole, most of these differences reflect morphological adaptations that were ventured upon in the grasses and have become widespread, but it is impossible to indicate what has failed to evolve or failed to succeed. This point is well developed by Clifford (1961) in discussing the possible number of symmetrical arrangements of floral organs that can be derived by reduction, and the number actually present in flowers in the family.

DIVERSITY OF REPRODUCTIVE SYSTEMS

The grasses display a wide variety of breeding systems that define their genetic architecture; these range from self-incompatible hermaphroditism through to dioecism. Hermaphrodite flowers are the most common, being absent from about 20 dioecious genera, and about 50 monoecious ones. The array of floral systems includes a marked andromonoecism and a lesser frequency of gynomonoecism; gynodioecism is rare. Heterostyly is unknown.

The extreme form of self-fertilization is seen in habitual cleistogamy, but autogamy or geitonogamy occurs in plants that flower chasmogamically, and self-compatibility is spread widely among tribes. Apomixis is recorded in about 30 genera, but apomixis, like autogamy and geitonogamy, is probably much underestimated.

An attempt at measuring the diversity of reproductive systems among the tribes, based on relatively simple criteria such as the presence of dioecism, monoecism, and apomixis (Table 1), indicates that all the major systems are present in very few tribes. The most diverse display lies in five tribes: Arundineae, Chlorideae, Eragrostideae, Festuceae, and Paniceae, and a further group of four tribes Andropogoneae, Aveneae, Hordeeae, and Pappophoreae is nearly as variable. However, apomixis is known in only one species in the Hordeeae; dioecism is known only in monotypic *Sohnsia* in the Pappophoreae; these data unduly imbalance Table 1. Deficiencies in the description of the flowers in many genera

make it difficult to interpret the breeding system present, and may be the cause of further imbalance in Table 1.

Among the tribes, and hermaphroditism apart, the most frequently occurring breeding systems are monoecism, including andro- and gynomonoecism, which is known in about 25 tribes, and cleistogamy which is known in about 20 tribes.

Reproductive Systems and Their Evolution

I propose to consider the reproductive systems in the family, and their possible, or even probable, evolution. This will be fraught with difficulties, not the least of which will be problems of finding true relatives, i.e., the correct placing of some genera in tribes, or the incomplete descriptions of flowers of many genera. Occam's razor will have to be used to prevent a plethora of inconsequential pathways.

The assumption that hermaphroditism is basic to the grass flower seems incontestable. Any deviation from hermaphroditism that results in separation of the two sexes—the evolution of various kinds of monoecism and dioecism—is one major departure. It is relatively easy to derive dioecism by postulating a gene for male sterility and another for female sterility, but valid genetic bases for their establishment, and for their maintenance, in natural populations are required as a variety of models show (Charlesworth & Charlesworth, 1978a, 1978b; Lloyd, 1974b, 1975a, 1976; Ross & Weir, 1976). The mutants must find the genetic milieu suitable for fixation or for the development of polymorphism, and develop in dioecism the linkages necessary to control segregation for sex. Similarly, the evolution of self-compatibility from self-incompatibility is easily described, but self-incompatibility must be selected against for self-compatibility to become fixed in a population. Habitual cleistogamy presumes self-compatibility, or at worst, the simultaneous evolution of self-compatibility and of changes in the flowering process.

I have chosen to present the steps that are envisaged in the evolution of any particular breeding system always as steps forward towards that system, i.e., as a progression. That regression is possible, e.g., from dioecism to monoecism by restoration of the alternate sex, is not commented upon unless the evidence suggests that this may have significantly occurred.

SEPARATION OF SEXES

The male and female organs may be separated from the close company of hermaphroditism in a variety of ways, but the simplest expression lies in dioecism and the more complex expression in the various forms of monoecism. Dioecism is less frequent than monoecism in the Gramineae.

MONOECISM, ANDROMONOECISM, AND GYNOMONOECISM

Monoecious plants are those where both sexes occur on the one plant but wholly or partly in different flowers; in monoecism male and female flowers occur on the same plant; in andromonoecism hermaphrodite (perfect) flowers and male flowers occur on the same plant; in gynomonoecism hermaphrodite flowers and

TABLE 2. Monoecism in the tribes of grasses; tribes in the order of Hubbard (1973).

Monoecism[a]	Andromonoecism[a]	Gynomonoecism[a]
	Bambuseae 3,[b]	
Atractocarpeae 3,[b]		
Phareae 1		
Olyreae 1		(Olyreae)
Buergersiochloeae 1		
Parianeae 1		
Centotheceae 3,[b]		Centotheceae[b]
Oryzeae 1		
Phyllorachideae 2		
	Arundineae 3,[b]	
	Danthonieae 3,[b]	
	Arundinelleae 2,[b]	
Isachneae 2,[b]	Isachneae[b]	Isachneae[b]
	Hordeeae 3	
		Festuceae 3,[b]
Aveneae 2,[b]	Aveneae 2,3,[b]	
	Phalarideae 2,3,[b]	
	Pappophoreae 3,[b]	
Eragrostideae 3,[b]	(Eragrostideae)	Eragrostideae[c]
	Chlorideae 2,[b]	
	Zoysieae 1	
Paniceae 2,[c]	Paniceae[b]	
Lecomtelleae 2,[b]		
Andropogoneae 2,[b]	Andropogoneae[c]	Andropogoneae[c]
Maydeae 2		

[a] 1 = 1-flowered, 2 = 2-flowered, 3 = 3- or more-flowered in the genera in which the monoecious states are known.
[b] Sex differentiation within spikelet.
[c] Sex differentiation both within and between spikelets.

female flowers occur on the same plant. The distribution of these systems among the tribes is shown in Table 2 where the tribes are arranged in the linear order of Hubbard (1973).

Because the step from hermaphroditism to andromonoecism or to gynomonoecism demands a single loss of fertility in each, and because both states are seen as pathways to monoecism, they may be considered first.

Gynomonoecism

Gynomonoecism is not frequent in the grasses; it is probably only successful in eragrostoid *Munroa* (Anton & Hunziker, 1978), but is known in a total of 8 genera among the six tribes listed in Table 2, viz., *Centotheca, Coelachne, Diandrolyra, Eriochrysis, Heteranthoecia, Munroa, Piresia, Poa,* (full references in Connor, 1980). For its origin, gynomonoecism demands a loss of male fertility in some flowers, but there must be a decrease in inbreeding to compensate for the reduction in male fertility (Charlesworth & Charlesworth, 1978b). Of the genera listed, there is evidence of self-compatibility only in *Poa*.

Another feature of gynomonoecism is that relatively fewer anthers must provide pollen for a relatively greater number of ovules, a contrast with andromon-

oecism (see p. 58). Anton (1978) gave some examples of the distribution of hermaphrodite and female flowers in Argentinian *Poa,* which show that there may be as few as 1 anther per ovule and up to 1.7 anthers per ovule.

Andromonoecism

Andromonoecism, hermaphrodite and male flowers on one plant, is widespread. This system is expressed in two major aspects; in one the two sex-forms occur within a single spikelet, and in the other differentiation for sex-form occurs between spikelets.

Andromonoecism is associated with the trend towards a single hermaphrodite terminal floret, a syndrome which is found in several tribes, but is at its fullest development in the biflowered spikelets of the large tribes Andropogoneae, Arundinelleae, and Paniceae.

Andropogoneae.—The Andropogoneae could well be the graveyard of those who wish to interpret the variety of andromonoecism expressed there! At the generic level one may choose between the 20 genera advocated by Roberty (1960) and a current estimate of about 80 genera.

In this tribe spikelets are usually paired, one pedicelled and the other sessile, and each is biflowered. The lower floret is usually neuter and the upper hermaphrodite [in abbreviated form S(OH) + P(OH)][3] but the andromonoecious form [S(OH) + P(OM)] is a common alternative. The range of sex-forms in Table 3 shows that andromonoecism may be expressed in several ways.

The essential first step in the evolution of andromonoecism is a loss of some female fertility; ovules develop a low genetic value, and those flowers become male. This step is said not to be easily established, and the view of Charlesworth & Charlesworth (1978b) is that, within the limits of their model, andromonoecism is unlikely to evolve as an outbreeding system.

The evolution of andromonoecism in the Andropogoneae would best be seen to have developed along the following pathway. There must first have been the evolution towards biflowered spikelets with hermaphrodite florets; and the development of paired spikelets. This was followed by the lower florets becoming male through the loss of female fertility. A subsequent mutation affecting the male fertility of those same lower florets would leave an apical hermaphrodite flower in each of the paired spikelets, and thus allow one modal form: S(OH) + P(OH). A further loss of female fertility, this time in the pedicelled spikelet only, would give rise to the andromonoecious form: S(OH) + P(OM). Such progressions would be slow to evolve.

The time at which the male and female sterility mutations arise during the evolution of the modal sex-forms allows the development of some of the andromonoecious variants: S(MH) + P(MH) of *Andropterum* where female sterility alone has operated in the basal flowers; S(MH) + P(OM) of *Sehima* where the sessile spikelets show an uncompleted series of gene actions; and S(MH) + P(MM) of *Robynsiochloa* with even fewer mutations.

[3] S = Sessile spikelet, P = pedicelled spikelet; H = hermaphrodite; M = male; F = female; O = neuter. Florets of a spikelet are included by brackets and in the order lower, upper. Symbols linked by + indicate presence on the one plant.

Table 3. Sex-forms in the Andropogoneae. H = hermaphrodite; M = male; F = female; O neuter. If triads are present there is usually an extra pedicelled spikelet. Homogamous pairs, where present, occur below the pairs shown here, and all flowers are M or O. Based on data from Jacques-Félix, Hubbard, Stapf, Pilger, Clayton.

Spikelet			Spikelet		
Sessile[a]	Pedicelled[a]		Sessile[a]	Pedicelled[a]	
	Andromonoecism			Gynomonoecism	
O H	O M	*Elionurus*	O H	O F	*Eriochrysis*
M H	O O	*Kerriochloa*			
M H	O M	*Sehima*			
M H	M M	*Robynsiochloa*			
M H	M H	*Andropterum*			
	Monoecism			Hermaphroditism	
M F	O O	*Triplopogon*	O H		*Cleistachne*
O F	O M	*Agenium*	O H	O O	*Bhidea*
M M	O F	*Sclerandrium*	O H	O H	*Erianthus*
M F, M M	M F, F F	*Lophopogon*			

[a] In each pair the left entry represents lower floret and right the upper floret of spikelet.

Internal evidence for the evolution of andromonoecism in this way in the Andropogoneae is sparse; pairs of spikelets in which both flowers of each are hermaphrodite is reported as a mutant in *Sorghum*, where a dominant gene controls restoration of fertility in flowers otherwise neuter (Webster, 1965). The closest approximation to paired spikelets of totally hermaphrodite flowers is in *Andropterum*: S(MH) + P(MH). The main evidence seems to lie in the presence of basal male florets, even in sessile spikelets (Table 3), indicating that the initial loss of female fertility occurred there. In the development of the spikelet the upper floret grows faster and is always larger (Bonnett, 1966).

Paniceae and Arundinelleae.—The Paniceae show a more general trend towards a reduced form of hermaphroditism because often the upper floret of a spikelet is a lone hermaphrodite flower.

In the biflowered Arundinelleae there is a common pattern of hermaphroditism in the upper floret, and various levels of emasculation and defeminization in the lower florets (Phipps, 1964). Spikelets are not paired in the Arundinelleae, though dimorphic florets are common. The Arundinelleae, it is assumed, followed a one-mutation pathway to andromonoecism because in only the lower floret is there any loss of sexuality.

Self-fertilization or self-compatibility is not very widely documented in the Andropogoneae, even with the inclusion of genera where cleistogamy is recorded (Connor, 1980). For the Paniceae the information is about equal, though *Paspalum* (Burson, 1979) and *Lasiacis* (Davidse, 1979) may be more firmly included as self-fertile genera. In the Arundinelleae there is no information on the compatibility relationship of any taxon; however, the anthers in *Arundinella pumila*, as described by Bor (1955), are very small and suggestive of cleistogamy, but anther length dimorphism occurs in *Arundinella*, e.g., anthers in male florets in *A. holcoides* and *A. ciliata* are about half as long as those in hermaphrodite

flowers. Anther length dimorphism is a feature of andromonoecism (Connor, 1980), but its relationship to self-fertilization or self-incompatibility, or to any aspect of pollination is unknown. On the whole, there may be sufficient self-compatibility to argue the development of andromonoecism in the ways outlined if andromonoecism aids in increased cross-fertilization.

Monoecism

Monoecism, separate male and female flowers on one plant, is exclusive to some tribes (Table 2). No other sex-form occurs in Buergersiochloeae, Lecomtelleae, Maydeae, Parianeae, Phareae, or Phyllorachideae. Monoecism, together with other sex-forms, occurs in: Andropogoneae, Atractocarpeae, Aveneae, Centotheceae, Isachneae, Olyreae, Oryzeae, and Paniceae. In general, a 1- or 2-flowered spikelet is a characteristic associate of monoecism.

In the Atractocarpeae, Isachneae, Aveneae, and some Paniceae monoecism occurs as separate male and female flowers in the one spikelet—perhaps the lowest form of strict monoecism. In the zizanioid Oryzeae, and in many instances in the Andropogoneae, there is separation of spikelets of different sex (see table 3 in Connor, 1980).

Among the bambusoid tribes Olyreae, Phareae, Parianeae, Buergersiochloeae, and Phyllorachideae the arrangement of sexually differentiated spikelets in an inflorescence is varied; thus there may be:

(i) sexes mixed in an inflorescence, often in paired spikelets with sessile female and pedicelled male as in *Maclurolyra* or *Pharus*;
(ii) sexes segregated on one inflorescence, females above and males below as in *Buergersiochloa*;
(iii) sexes completely segregated in pairs of racemes as in *Ekmanochloa*;
(iv) sexes completely segregated with male flowers terminal above, and axillary females below as in *Humbertochloa*.

Internal evidence that a gynomonoecious pathway to monoecism is at least possible in the Olyreae, is available from the work of Soderstrom & Calderón (1974) who showed that pedicelled spikelets with an hermaphrodite organization, and sessile female spikelets occur in *Diandrolyra*, and Bahian *Piresia*. The pedicellate "hermaphrodite" spikelets, however, fall soon after pollen is shed; effectively, monoecism is achieved. Regardless of this precise pattern, the gynomonoecious pathway is evident. Charlesworth & Charlesworth (1978b) describe this system as involving firstly a reduction in male fertility in some hermaphrodite flowers to produce female flowers and thus gynomonoecism, followed by a reduction in female fertility of the hermaphrodite flowers to produce male flowers, a sequence H → H + F → M + F.[4] Correlatively with the sterilities there must be a large reduction in inbreeding. Monoecism is seen by the Charlesworths as an uncommon development in flowering plants, and they emphasize that it may

[4] H = Hermaphrodite, M = male, F = female; symbols linked by + indicate presence on the one plant.

well be necessary for two or more mutations to reduce female fertility to such an extent that it will yield a male flower. There is no linkage between sterility genes.

Redistribution of male and female flowers into the patterns indicated above would seem to flow easily from a simple, terminal inflorescence of flowers of both sexes to the advanced form of "terminal male and axillary female" inflorescences. This redistribution could be developing during the sequence of mutations eliminating ovule production of those flowers that were still hermaphrodite. Not every known sex-form is accounted for: e.g., in *Lithachne* the axillary inflorescence may contain one apical female-flowered spikelet and several male-flowered spikelets below (Hitchcock & Chase, 1917; Soderstrom & Calderón, 1974), and in *Phyllorachis* the terminal inflorescence bears male flowers above and female flowers below, while the axillary inflorescence is totally female (Hubbard, 1939). These examples and others represent possible phases in the development of monoecism; it is unreasonable to expect evolution conveniently to match every model.

The tribe Maydeae is strictly monoecious; here male inflorescences are found above the female ones, there are sessile and pedicelled spikelets in unisexual pairs, and a tendency towards axillary inflorescences of female flowers. The tribe is alternatively included in the strongly andromonoecious Andropogoneae; any projected pathway to monoecism would seem to be that through andromonoecism, followed by redistribution of male flowers to terminal inflorescences, and with hermaphrodite flowers being distributed below the males, or to axillary positions. A second mutation causing male sterility in the hermaphrodite flowers of axillary inflorescences would produce female flowers only.

In the Zizanieae, or zizanioid Oryzeae, males are present in terminal inflorescences, and females in leaf axils below as in *Luziola*, or are distributed on one inflorescence as female flowers above the male flowers as in *Zizania*. The pathway to monoecism is expected to be the same as that for the bambusoid tribes, though there is no internal supporting evidence; and *Zizania latifolia* by not conforming exactly to the "female above, males below" diagnosis but in having inflorescences less perfectly arranged (Bannikova, 1976), in fact offers some evidence that sex-forms are being redistributed. The Zizanieae are self-fertile (East, 1940), but protogynous (Weir & Dale, 1960).

Monoecism with the sexes differentiated within a spikelet involves the same genetics as the other monoecious forms. Between-floret differentiation occurs in the Atractocarpeae, Centotheceae, Eragrostideae, Isachneae and Lecomtelleae, in one or two genera of the Andropogoneae, and Argentinian *Hierochloe* (Aveneae).

In both the Centotheceae and the Atractocarpeae there are several florets per spikelet. The sex-forms in the Centotheceae range from hermaphroditism through gynomonoecism to monoecism as in: *Orthoclada* H; *Centotheca* H + F; *Calderonella* M + F and *Zeugites* M + F. In *Zeugites* and *Calderonella* the lowest floret only is female; but in *Centotheca* the upper floret is female. Neuter flowers may be present in some members of the Centotheceae, so that in *Chevalierella* the lowest floret is hermaphrodite and the upper neuter; in *Chasmanthium* the two lowermost florets are neuter and the remainder hermaphrodite. The internal evidence from *Centotheca* would point to a gynomonoecious origin of monoecism.

Blepharidachne (Eragrostideae) has three monoecious species and a fourth, *B. kingii,* which is hermaphrodite. The pathway here to monoecism is via andromonoecism. Only one seed is formed in the four-flowered spikelet—that in the penultimate floret which has a functional gynoecium. Anthers may number 1 or 2 or 3 depending on the species (Hunziker & Anton, 1979). In *Atractocarpa* and *Puelia* the female flower is apical in the spikelet, the flowers below being male and/or neuter; most related bambusoid genera have hermaphrodite flowers. *Hierochloe* (Aveneae) in Argentina is monoecious (De Paula, 1975), but most species in that genus are andromonoecious. Andromonoecism is the appropriate pathway to monoecism in these genera.

In the group of related tribes Isachneae, Lecomtelleae, and Paniceae, sex differentiation mostly occurs within the spikelet: usually the lower flower is male and the upper female, though in *Lecomtella* there are some spikelets with two male florets and others with one male and one female flower. In the Isachneae because gynomonoecism is present as in *Coelachne* and *Heteranthoecia* (p. 51), and andromonoecism in some species of *Isachne* (Bor, 1952), there is internal evidence of two possible pathways to monoecism. *Lecomtella,* with an excess of male flowers in some spikelets (Stapf, 1927), may represent what Charlesworth & Charlesworth (1978b) refer to as a reduction in female fertility through a mutation increasing the ratio of male to female flowers, making the bisexual form more malelike. Such a character is indicative of an andromonoecious origin. But the Lecomtelleae is a tribe distant from the main stream of evolution in the Paniceae (Brown, 1977), and it would be unwise to transfer too much influence from it to the Paniceae. In the Paniceae, *Chamaeraphis* and *Pseudoraphis* are monoecious. An andromonoecious pathway is indicated for members of these tribes. *Hygrochloa,* aquatic, monoecious, newly recognized, and the only genus in the Paniceae with male and female spikelets separately distributed on the inflorescence, is of remote affinity in the tribe according to Lazarides (1979).

Redistribution of sex-form is associated with the most highly developed forms of monoecism; the change from a shoot with a terminal inflorescence to one incorporating axillary inflorescences as well, seems one opportunity in the evolution of monoecism. It necessitates a particular morphogenesis, but it seems to be the next most successful evolutionary step in inflorescence development. It is also a very deliberate step towards the possibility of dichogamy—one feature that can be associated with attempts to promote allogamy.

The evolutionary pathways to monoecism backed by genetic models of Charlesworth & Charlesworth (1978a, 1978b) seem not unreasonable even though they are heavily weighted in the direction of the avoidance of inbreeding by promotion at least of some way of ensuring outcrossing.

Among the monoecious tribes, self-compatibility is known in the Andropogoneae, Aveneae, Eragrostideae, Maydeae, and Paniceae, but nothing is recorded of the compatibilities of the Buergersiochloeae, Centotheceae, Olyreae, Parianeae, Phareae, and Phyllorachideae (see list in Connor, 1980). Self-compatibility and the associated inbreeding depression are seen by Charlesworth & Charlesworth (1978a, 1978b) to be essential to the pathways they outlined. There is sufficient self-compatibility to satisfy that requirement. Should any of these mon-

oecious genera be self-incompatible, alternative genetic explanations must be sought.

Excess Maleness

"Chez beaucoup d'espèces tropicales et surtout chez les Andropogoneae, comme leur nom l'indique, il y a androphilie c'est-à-dire nette prédominance des éléments mâles" (Jacques-Félix, 1962). Clifford (1961) might see these extra anthers as offsetting a reduction to three stamens per flower, because for a wind-pollinating group this common reduction is seen to be disadvantageous. Cruden (1977) and other authors would refer to this in general as producing very high pollen-ovule ratios. Charlesworth & Charlesworth (1978b) might see this predominance of male flowers as part of a projected sequence towards monoecism and/or dioecism where at some stage plants are "more malelike" in that they possess many male flowers. The loss of the ovule function suggests that pollen is of high genetic value and that there have been substantial increases in male fertility; both these are anticipated from their models.

In the Andropogoneae the size of the increase in male fertility is measurable in some taxa in two ways: (i) the number of solely male flowers relative to hermaphrodite flowers and (ii) the relative sizes of the anthers found in both. Neither of these is the pollen-ovule ratio of Cruden though they contain its essentials. Differences in size of anthers, depending in which flower they occur, are given for *Diheteropogon*, *Exotheca*, and *Hyperthalia* by Connor (1980). *Euclasta condylotricha* is also described as dimorphic for anther size, those of the male flower being much longer than those of the hermaphrodite flower (Jacques-Félix, 1962); I am unable to find any absolute measurements. There must be other equivalent data for the tribe though I am unaware of them.

The relative number of anthers per ovule in a pair of spikelets can be readily calculated from data in Table 3. For many genera with the form S(OH) + P(OM) there are three anthers in the male flower and three in the hermaphrodite flower to 1 ovule, i.e., 6 a : 1 ov. From the form S(OF) + P(OM) the ratio is 3 a : 1 ov, as is the ratio in forms with pairs S(OH) + P(OH).

Where there are pairs of homogamous male spikelets subtending the "fertile" part of an inflorescence, there is an immediate increase in anther : ovule ratio. Thus in a genus like *Elymandra* in one raceme with three ovules there may be something of the order of 28 to 46 anthers—a range of 9 a : 1 ov to 15 a : 1 ov (see fig. 240 in Jacques-Félix, 1962). Where anther size polymorphism occurs as in *Hyperthelia edulis* (Hubbard, 1950 as *Hyparrhenia*) each ovule in a raceme is accompanied by three anthers up to 9 mm long in the sessile spikelet, six anthers up to 19 mm long in the pedicelled spikelets, and six anthers up to 4 mm long in the homogamous pair. In *H. colobantha*, the upper raceme of the pair is reduced to one pedicelled, male spikelet (Clayton, 1967); the ratio here becomes 18 a : 1 ov for the two racemes. Clayton did not describe anther sizes.

The data in Weatherwax (1926) for Oriental Maydeae give anther : ovule ratios for: *Chionachne* 12–20 a : 1 ov, *Coix* 180–600 a : 1 ov, *Polytoca* 30–60 a : 1 ov.

Among the tropical Bambusoideae monoecism is well established in the Olyreae; Soderstrom & Calderón (1979a) and Calderón & Soderstrom (1973) indicate

the frequencies of male and female flowers in some genera. In *Maclurolyra* for example, the terminal inflorescence bears one female flower and close by 4–6 males giving 12–18 a : 1 ov, and below these may be several pairs of spikelets with one female and one male flower each, i.e., 3 a : 1 ov. *Bulbulus* is similar; (this genus has been renamed *Rehia* by Fijten, 1975). In *Arberella flaccida* the ratio is 15–24 a : 1 ov, in *A. costaricensis* 24–30 a : 1 ov, in *A. dressleri* 18–24 a : 1 ov.

In *Strephium* and *Raddia*—where the two sexes are borne on separate inflorescences—there are many more male flowers than female in *Strephium*, but fewer male flowers than female inflorescences in *Raddia*.

Pariana, the monotypic genus of the Parianeae, may bear 75–105 a : 1 ov, or even more.

For cross-fertilization pollen must firstly reach a receptive stigma, only then can the compatibility specificity be expressed. Wind-pollination is a very unspecialized pollination system and in the Gramineae is linked to an efficient and specialized incompatibility system. High pollen : ovule ratios are characteristic of anemophily. The Andropogoneae, Olyreae, and Maydeae that have been discussed, all possess high or relatively high, anther : ovule ratios (the precise pollen : ovule ratios I am unable to calculate). Yet the Maydeae are self-fertile (East, 1940) and so are many species of the Andropogoneae.

For the tropical Olyreae, wind pollination is very difficult because of the extreme stillness of their forest floor habitat (Davis & Richards, 1933; Whitehead, 1969; Soderstrom & Calderón, 1971, 1979b); further, the leaves cover or protect the abundant axillary inflorescences, limiting what wind action there is. For the herbaceous bambusoids, therefore, the excess of male flowers may be the guarantor of pollination by an inadequate anemophily or by the secondary development of entomophily.

This explanation cannot be applied to the Andropogoneae of the savanna and of tropical areas elsewhere as far as I know. The Andropogoneae may just need abundant pollen to overcome problems of effective wind pollination; if so, they differ significantly in this respect from many other grasses.

DIOECISM

Dioecism is not a major phenomenon in the Gramineae, as dioecious species are known from 20 oligotypic genera only. Among the tribes, dioecism is found in the Aeluropodeae, Arundineae, Chlorideae, Eragrostideae, Festuceae, Paniceae, and Pappophoreae (Table 4). Gynodioecism, a specialized form of dioecism, if included here does not alter the number of tribes with dioecious taxa. Two tribes are significantly dioecious, the Aeluropodeae and the Chlorideae; in the former there are five dioecious genera and in the latter there are seven. Elsewhere one or two genera in large tribes is characteristic, e.g., *Spinifex* and *Zygochloa* are the only two dioecious genera in the Paniceae (Blake, 1941), and only *Neeragrostis* (Nicora, 1962) and *Scleropogon* (Reeder, 1969) in the Eragrostideae.

In most genera with dioecious taxa the spikelets are multiflowered; exceptions are the two biflowered panicoid genera *Spinifex* and *Zygochloa*; none is single-flowered.

For the Arundineae where *Gynerium* is dioecious and *Lamprothyrsus* has

TABLE 4. Dioecious genera; references in Connor (1980).

Aeluropodeae:	*Allolepis, Distichlis, Jouvea, Monanthochloe, Reederochloa.*
Arundineae:	*Cortaderia,*[b] *Gynerium, Lamprothyrsus.*
Chlorideae:	*Bouteloua,*[b] *Buchloe,*[a] *Buchlomimus, Cyclostachya, Opizia,*[a] *Pringleochloa,*[a] *Soderstromia.*[a]
Eragrostiueae:	*Neeragrostis, Scleropogon.*
Festuceae:	*Festuca* (subgenus *Leucopoa*),[c] *Poa.*[a,b]
Paniceae:	*Spinifex, Zygochloa.*
Pappophoreae:	*Sohnsia.*

[a] Occasionally monoecious.
[b] Also gynodioecious.
[c] Correcting entry in table 1 of Connor (1980).

been so at some time—and gynodioecism is active in *Cortaderia* (Connor, 1974)—a gynodioecious pathway to dioecism is evident. Andromonoecism is also present in the tribe in *Phragmites* and *Gossweilerochloa*; *Gossweilerochloa,* a monotypic genus from Angola has lower florets hermaphrodite and upper florets male (Renvoize, 1979). Neither it nor *Phragmites* persuades me that a route through andromonoecism to monoecism and thence to dioecism is likely in the tribe.

The suggested pathway towards dioecism in the Arundineae via gynodioecism involves firstly the establishment of male sterility gene(s)—usually recessive—in some hermaphrodite plants giving rise to hermaphrodite and female plants, i.e., gynodioecism. This is followed by a mutation—usually dominant—for female sterility which acts in the hermaphrodites thus giving male plants. Such a combination of alternating gene action will lead to sets of linked genes controlling sex, and to heterogametic male plants. Charlesworth & Charlesworth (1978a) emphasize that this process is a long and extremely slow one. Also important is that self-compatibility and a high level of self-fertilization occur in the group where evolution of dioecism is taking place, and that there is some increase in pollen output by the males. In New Zealand species of *Cortaderia,* at least, there is abundant self-compatibility in hermaphrodite plants (Connor, 1974).

The tribe Chlorideae offers perhaps the greatest concentration of dioecious genera, but Reeder (1969) pointed out that with the exception of *Buchlomimus* and *Cyclostachya,* plants of *Buchloe, Opizia, Pringleochloa,* and *Soderstromia* may at times be monoecious. Systems currently known in the Chlorideae, apart from dioecism, include hermaphroditism, andromonoecism, and possibly gynodioecism in *Bouteloua chondrosioides* (Reeder & Reeder, 1966; Reeder, 1969). On the basis that monoecism is recurrent among the dioecious taxa (Reeder, 1969), the probable pathway to dioecism for the Chlorideae is through monoecism, that is, along pathways to monoecism that have already been discussed (p. 54). It is clear that this pathway is much longer than the gynodioecious one, necessitating firstly the development of andromonoecism as the consequence of reduction in female fertility in some flowers, and subsequently a further reduction in male fertility of the remaining hermaphrodite flowers to produce female flowers and thus the monoecious state. As was discussed earlier (p. 52), low genetic values in the ovules of the hermaphrodite flowers that become male is the major factor. Subsequent steps producing more malelike and more femalelike phenotypes ultimately yield the male and female plants of a dioecious population. Dioe-

cism originating in this way will be controlled by sets of linked genes and be the result of an extremely slow evolutionary process. Genetic conditions and selection pressures under which such systems could evolve are detailed by Charlesworth & Charlesworth (1978b). In taxa following this sort of pathway, males and females with traces of the activity, not just the morphology, of the opposite sex may be found (Lloyd, 1975b). In the Chlorideae cleistogamy is common and may be one of the self-fertilizing systems being selected against by dioecism.

In the closely related Eragrostideae there are two dioecious genera, *Neeragrostis* and *Scleropogon*. There is internal evidence from within the tribe to indicate a pathway towards dioecism, and the proposition of an escape from inbreeding is quite strong, because self-compatibility and cleistogamy are well established there (see table 8 in Connor, 1980). *Ectrosia*, which is commonly cleistogamous, may have a large number of male flowers—making it andromonoecious—or those flowers may be neuter (Hubbard, 1936). *Munroa* is gynomonoecious in most species; *Blepharidachne*, on the other hand, is hermaphrodite in one species and monoecious in three others; on these bases, pathways through monoecism are probable for the dioecious genera.

The gynomonoecious origin of dioecism differs only in initial detail from the andromonoecious pathway just described for the Chlorideae. Initially a male sterility gene acts in some flowers to produce plants with female and hermaphrodite flowers. Subsequent steps invoke female sterility in the hermaphrodite flowers to produce monoecious plants; from then on the process is that described above. The difficulties alluded to by Charlesworth & Charlesworth (1978b) are unchanged by the chronology of genes reducing fertility.

In the Aeluropodeae five genera (or more) are dioecious (Table 4). Yet there is no internal evidence to suggest a pathway to dioecism; *Aeluropus* itself is hermaphrodite. The Pappophoreae are distinguished on the other hand by hermaphroditism except for the monotypic dioecious genus *Sohnsia* for which no clear pathway to dioecism is indicated from the floral forms of other genera in the tribe; what is clear is that cleistogamy is a feature of many pappophorean genera (Connor, 1980).

For *Poa* (Festuceae) pathways to dioecism are not difficult to suggest, though none is explicit from internal evidence. In *Poa* there are gynodioecious species which would suggest this direct pathway, but gynomonoecism is also present and suggests that the much longer monoecious pathway is possible. The choice may lie in recognizing that two pathways could operate. In *Festuca*, subgenus *Leucopoa*, there is sporadic dioecism; no particular pathway is evident.

In the Paniceae *Spinifex*, and its segregate *Zygochloa*, are the only dioecious genera; they are also the only dioecious genera in the subfamily Panicoideae. The floral arrangement in the biflowered Paniceae—lower floret male or very often neuter, upper floret hermaphrodite—indicates andromonoecism or alternatively hermaphroditism. A possible pathway to dioecism could involve either monoecism or gynodioecism. Monoecism is a low frequency phenomenon in the tribe, occurring in *Hygrochloa*, *Chamaeraphis* and *Pseudoraphis* only. Gynodioecism is unknown. The gynodioecious pathway is simpler than the monoecious one because the action of the necessary genes seems more direct, but simplicity is unlikely to be the guarantor of an evolutionary pathway.

The pathways that have been discussed as being the most probable in the evolution of monoecism and dioecism depend to a large extent on the presence of self-compatibility and self-fertilization. This may appear to suggest that self-compatibility was, or is, very widespread in the family. It is. But if the predecessors of 20 dioecious genera and of 45–50 monoecious genera evolved as a reaction to self-compatibility, that number is very small relative to the 600–700 genera in the family.

Willson (1979), who does not accept that the advantages of obligate outcrossing ". . . present as powerful and all pervasive a force as seems to be commonly assumed," described an ecological gradient towards dioecism. Sexual selection along one gradient is seen ultimately in an ". . . overwhelming reproductive success of some individuals functioning as say, males; selection then would favor the allocation of food resources entirely to male flowers and increase their success still further." Genetic advantage to dioecism is not excluded, and Willson suggests that both genetic diversity from recombination, and sexual selection were contributors to the evolution of dioecism.

HERMAPHRODITISM

Variation in the breeding system of hermaphrodite plants is achieved at the genetic level by mutations affecting compatibility relationships, and at another level by changes in the timing of presentation of pollen and of receptive stigmata. Dichogamy does not invariably guarantee a within-plant delay in the maturation of male- and female-bearing organs or in their presentation, often because of the sequential emergence of inflorescences on the one plant (see Burton, 1974).

An important evolutionary step in the family is the development of self-compatibility, a step independent of changes in levels of ploidy (Lundqvist, 1975). Self-compatibility has been identified in about 100 genera in the family (Connor, 1980).

CLEISTOGAMY

Self-fertilization is extensively used as a normal method of reproduction especially in annuals (Stebbins, 1957), and in the specialized form of cleistogamy, self-fertilization has been reported in 18 tribes and from about 70 genera (table 8 in Connor, 1980). This is most probably an underestimate if one judges from the illustrations of so many flowers, and from the anther sizes given in some descriptions. Mostly cleistogamy is facultative, though some taxa are predominantly cleistogamic and some few are known only in the cleistogamic form. Some tribes have greater concentrations of cleistogamous genera than others, e.g., in the Eragrostideae 11 genera bear cleistogamic flowers, and there are 9 genera in the Paniceae, 7 in the Andropogoneae, and 6 in each of the Aveneae, Danthonieae, and Festuceae.

The evolution of cleistogamy depends initially on the presence of self-compatibility. Morphological features often associated with nonanthesis, e.g., reduced anther and lodicule sizes, or even the loss of lodicules, are probably interpretable as precocious development (Lord, 1979). In addition to cleistogamous flowers in terminal inflorescences, cleistogamous inflorescences may be hidden

in leaf axils—the cleistogenes of Chase (1918) which I prefer to call clandestine inflorescences or spikelets.

Clandestine inflorescences are smaller than aerially borne inflorescences, and in the most reduced form are single spikelets only; they are probably precociously developed, because in *Stipa leucotricha* Dyksterhuis (1945) could record them in plants about six months old. In the same species he found that clandestine spikelets were advanced in seed setting before anthesis had begun in aerial inflorescences.

This specialized form as clandestine spikelets is more advanced than facultative cleistogamy in aerial inflorescences. In all known examples they are a secondary form of seed setting, but usually produce in total fewer seeds than aerially borne inflorescences, though as Hubbard (1933) pointed out, clandestine spikelets may occur in all leaf axils of *Cleistochloa*; in *Microlaena polynoda* very many leaf sheaths are swollen with spikelets (Connor & Matthews, 1977).

Clandestine axillary spikelets are known in 13 genera, viz., *Aristida, Calyptochloa, Cleistochloa, Cleistogenes, Cottea, Danthonia, Diplachne, Enneapogon, Microlaena, Muhlenbergia, Sieglingia, Stipa, Triplasis*; full references are in Connor (1980). Aerial inflorescences in all these genera bear both cleistogamic and chasmogamous florets, except *Cleistochloa* where only chasmogamic flowers are known (Hubbard, 1933).

At another level of development, cleistogamy is found in subterranean spikelets; these spikelets are most probably more highly evolved than those that arise from the conversion of an axillary vegetative bud to a reproductive one as in clandestine spikelets. Subterranean spikelets are reported from four genera only: *Chloris* (Chlorideae), *Amphicarpum* and *Paspalum* (Paniceae) and *Eremitis* (Parianeae). In *Eremitis* these subterranean spikelets were only recently discovered (Soderstrom & Calderón, 1974), but the well-known annual *Amphicarpum purshii* was subject to experiment by McNamara & Quinn (1977) who showed the high level of dependence by this taxon on subterranean spikelets.

Cleistogamy was suggested by Clifford (1961) as one possible response following a change from entomophily to anemophily in the Gramineae. For cleistogamy to develop the sole requirement is that it must be preceded by a mutation to self-compatibility; this mutation and the development of ancillary features of the cleistogamic habit were unlikely to be simultaneous.

Cleistogamy occurs in plants at both high and low latitudes, at high and low altitudes, in forest and grassland, in annuals and perennials, in archaic tribes and in advanced tribes, in tribes significantly associated with monoecism and dioecism and in tribes that are not. Cleistogamy is known to be a response to differences in daylength, to be a response to soil moisture variation, to co-occur simultaneously with chasmogamy in the same plant, to have differing modes of pollination, and to occur before or after inflorescence emergence. Many of these responses coincide with ecological demands, but ecological or ecophysiological interpretations do not totally account for all occurrences of cleistogamy and certainly not for simultaneous cleistogamy and chasmogamy on the one plant.

Cleistogamy, like other breeding systems, is one evolutionary possibility open to the grasses; they adopted it as a specialized self-compatibility system and later

adapted it in the form of axillary clandestine spikelets, and to a lesser extent in subterranean spikelets. Its frequency is a measure of its success.

APOMIXIS

Departures from and variants on hermaphroditism are pathways open to the grasses, and a departure from sexual reproduction yet another. I do not propose to discuss proliferation though it is important at high latitudes, and intend only very briefly to discuss apomixis because one either discusses embryological detail, or environmental control, or the genetics of inheritance, or invariability in the next generation. All these topics have been most adequately treated elsewhere (Stebbins, 1941; Gustafsson, 1946–1947; Nygren, 1954, 1967; Battaglia, 1963; Connor, 1980).

The distribution of apomixis in the grasses (Table 5) is of no significant value in any systematic interpretation of tribes or lesser ranks. In the Andropogoneae, Paniceae, and closely related tribes, apomixis has been reported in about 20 genera, something of the order of 10% of the genera.

It is significantly absent, or unrecorded, in the Bambusoideae as interpreted by Soderstrom & Calderón (1979b). The Arundinoideae, which always seems central to any discussion on the family, includes two apomictic genera; there are three in the Festucoideae, and three in the Chloridoideae-Eragrostoideae.

At the genetic level, somatic apospory is more frequent in the Panicoideae than elsewhere, but neither it nor gonial apospory (diplospory) is exclusive to any subdivision of the family. The absence of pollen stimulation, i.e., nonpseudogamy, is known only in the five nonpanicoid genera: *Calamagrostis, Cortaderia, Lamprothyrsus, Nardus, Poa*; autonomous apomixis is a more independent state than pseudogamy but possesses little scope for versatility.

Apomixis is associated with monoecism in *Tripsacum* only, and with dioecism in the special cases where females alone are now known—*Cortaderia* and *Lamprothyrsus*. Apomixis occurs in self-incompatible and self-compatible hermaphroditic flowers. In the Andropogoneae it has often replaced andromonoecism. Apomixis is clearly a recent development in the Gramineae and coincident with the universal observations of hybridization and polyploidy.

In many genera apomixis is readily reversible with sexual reproduction because apomixis is rarely totally obligate. Such a capability seems more advantageous than that in the nearest approximation, that is, in the switch from cleistogamic to chasmogamic flowering. Whether the reversals from dioecism as reported for the Chlorideae by Reeder (1969), or any other reversal, is as frequent or as balanced as the sexual-asexual switch among apomicts is unknown.

RESPONSE TO THE BREEDING SYSTEMS

Is there an optimal breeding system for the Gramineae? The question contains a teleological element, but teleology is necessary to allow the formulation of satisfactory hypotheses. Theory suggests two possibilities for maximum heterozygosity, for recombinants, and for maximum capacity to react to major environmental changes; these are dioecism and multiallelic incompatibility genes—

TABLE 5. Apomixis in the tribes of grasses; tribes in the order of Hubbard (1973); references in Connor (1980). + = present; − = absent; SI = self-incompatible; SC = self-compatible; MS = male sterile.

Tribe	Apospory Gonial	Apospory Somatic	Pseudogamy	Genera	Sex-Form
Arundineae		+	−	2; *Cortaderia, Lamprothyrsus*	in MS only
Hordeeae	+		+	1; *Agropyron*	hermaphrodite; SC
Festuceae	+	+	+/−	1; *Poa*	hermaphrodite or MS
Aveneae		+	+	1; *Hierochloe*	andromonoecious
Agrostideae	+		+/−	1; *Calamagrostis*	hermaphrodite; SI, SC
Nardeae	+		−	1; *Nardus*	hermaphrodite or MS
Eragrostideae	+		+	1; *Eragrostis*	hermaphrodite
Chlorideae		+	+	2; *Bouteloua, Chloris*	hermaphrodite; SI
Paniceae	+[a]	+	+	9; *Cenchrus, Panicum,* etc.	andromonoecious or hermaphrodite
Anthephoreae		+		1; *Anthephora*	andromonoecious
Andropogoneae	+[b]	+	+	9; *Bothriochloa, Dichanthium,* etc.	andromonoecious
Maydeae	+		+	1; *Tripsacum*	monoecious

[a] Reported in *Paspalum* only.
[b] Reported in *Saccharum* only.

the *S* genes. Other systems seem less adequate on a variety of grounds. Heterostyly is absent.

In the evolution of the breeding systems discussed so far, there is a strong element of the avoidance of self-fertilization especially through monoecism, including andromonoecism and gynomonoecism, and protandry and protogyny in hermaphrodite flowers. Monoecism of itself is not necessarily a breeding system that promotes the avoidance of self-fertilization because self-fertile taxa will remain self-fertile after the evolution of monoecism. Monoecism increases the opportunity for dichogamy but does not generate it.

Andromonoecism is established in one of the more successful groups of the world's grasses, the Panicoideae; the andromonoecious habit has no special merit as a breeding system unless increased male fertility, measured in terms of pollen production, is demanded by the genetic situation. In the Andropogoneae the tendency to become exceedingly male, and consequently with fewer seed-bearing florets, is one of the significant enigmas of the tribe (Clayton, 1967; Olorode & Baquar, 1976; Connor, 1980). Charlesworth & Charlesworth (1978b) do not see andromonoecism evolving as an outbreeding device.

Gynomonoecism, occuring only sporadically in five or six tribes, has only been studied as a breeding system in *Poa annua* (Ellis et al., 1971; Ellis, 1974). Without strong dichogamy, self-fertilization is unlikely to be totally avoided. Gynomonoecism has its main significance as one point on an evolutionary pathway to monoecism, but the evidence from within the tribes in which monoecism occurs, does not suggest that any of the highly evolved monoecious sex-forms is related to currently gynomonoecious groups except in *Diandrolyra* (see p. 54).

Hermaphroditism is very often associated with self-compatibility, and experimentally verified self-fertilization without significant inbreeding depression has

been established in 45 genera; to these must be added those genera where cleistogamy is easily verified, bringing the total to about 100 genera (see Connor, 1980). In many of these genera there are self-incompatible species as well, e.g., in *Bromus, Lolium, Phalaris,* and *Poa.* It is sufficient to indicate that the mutation to self-compatibility is, or was, a frequent development, and because this derived self-compatibility is present in simple and advanced tribes, it may be assumed that the tendency to mutate is not much younger than the tribes themselves.

Apomixis is generally interpreted as a system lacking evolutionary advantage, but as it is more frequently facultative than obligate, there are opportunities for the formation of new recombinants. Should mitotic recombination as discussed by Stern (1936), Evans & Paddock (1976), and Harrison & Carpenter (1977) be of widespread occurrence, some of the opprobrium attached to apomixis may be withdrawn, and this system may be admitted into the group of genetically diverse reproductive systems.

Best suited to anemophily as the pollen dispersal system, and to the requirement for the maximum number of recombinants, are dioecism and multiallelic incompatibility.

DIOECISM

Dioecism leaves little option but for obligate cross-pollination; the assumption is usually made that all pollinations are compatible. In strict dioecism each sex-form makes an equal genetic contribution to the next generation, but there must also be: (i) chromosomal sex determination, or its equivalent, (ii) an efficient pollen transfer mechanism, and (iii) a normal sex-ratio. Should there be an ecological differentiation favoring one sex over the other as shown by Freeman et al. (1976) for *Distichlis spicata* and for other families by Lloyd & Webb (1978), then the distribution of the sex-forms, both in number and place, may affect the efficiency of dioecism.

Dioecism in the Gramineae is at a low frequency—about 20 genera from seven tribes. The genetics of dioecism is unexplored in the family. One count of males and females in *Buchloe dactyloides,* that of Schaffner (1920), whose results indicated .50M : .50F in the field, this together with a small sample of seed giving .50M : .50F, constitute the major published facts of dioecism. Voigt et al. (1975) indicated that with selection a high frequency of female plants could be obtained in *B. dactyloides* but presented no details. Based on quadrat counts of inflorescences, frequencies in the rhizomatous grass *Distichlis spicata* are: .49M : .51F, but the sexes are not distributed at random (Freeman et al. 1976). In *Bouteloua chondrosioides* .31M : .69F was obtained from seed (Reeder & Reeder, 1966); this is a very wide departure from .50M : .50F. Should *B. chondrosioides* be gynodioecious these valuable results are uninterpretable because of the uncertainty about the sex-form of the seed parents. There is no doubt, however, that there is an excess of female plants—57M and 118F—among the three families raised from seed; Lloyd (1974a) discusses the topic of female predominant sex-ratios.

Differentiation associated with dioecism is better known. There are, for example, more florets per spikelets in male plants than in females in *Jouvea* and

Monanthochloe (Villamil, 1969; Weatherwax, 1939), and the greater number of male florets is assumed to be related to the supply of pollen to female spikelets that are hidden among the leaves. In *Jouvea* the males are borne well above the leaves, but in *Monanthochloe* the male flowers, like female flowers, are hidden. The fit to the model is imperfect.

The less specialized form of dioecism, gynodioecism, is restricted to two genera, *Cortaderia* and *Poa*, but there are three genera if *Bouteloua* is admitted. In *Poa* there is an array of species (see summary in Connor, 1980); in *Cortaderia* there are about 20 gynodioecious species and 5 that are apomictic (Connor, 1974; Philipson, 1978; Costas-Lippmann, 1979).

In *Cortaderia* hermaphrodite plants are heterogametic. Some hermaphrodites are self-compatible, but South American *Cortaderia selloana* behaves for the greater part as a dioecious species. Hermaphrodites are self-incompatible, and at most produce a few, poorly germinable seeds; their contribution to subsequent generations is chiefly as pollen parents. Natural populations do not depart from .50M : .50F. The genetics of male sterility are complex, though the behavior in natural populations is simple; thus .50M : .50F is reproducible in nature because female plants are pollinated by plants themselves derived from crosses of the same kind, and therefore heterozygous. Both Lloyd and I (Connor, 1974; Lloyd, 1976) have shown how .50M : .50F is maintained in natural populations.

Male-fertility is dominant over male-sterility, and it is possible in experiments to produce populations of male plants. In some experimental crosses, however, the frequency of females may be greatly in excess of the 50% so commonly found in my experiments and in natural populations (Connor, 1974), and reach 80%. I have no ready genetic model to fit these data, but am attracted on the one hand to explanation for imbalanced sex ratios based on meiotic drive (see Sweeney & Barr, 1978; Hastings & Wood, 1978), and on the other, to cytoplasmic interaction.

This discussion of a subdioecious species is to present data of the kind that is needed for dioecism. Elsewhere I have discussed the self-compatible and strictly gynodioecious New Zealand species of *Cortaderia* (Connor, 1965, 1974).

The small number of dioecious taxa and their distribution among tribes may be an indication that dioecism has been found wanting as an evolutionary possibility within the family. Relative to other families where dioecism is present, dioecism in grasses—about 3% of the genera—is at a low frequency. The greatest concentration of dioecious grasses is in the New World (Reeder, 1969), and it will be interesting to see if the ecological selection for dioecism suggested by Willson (1979) can be invoked to explain any features associated with this pattern; some features of distribution of the taxa are clearly related to major ecological characters.

Gynodioecism is so rare in the family as to not merit much attention as an optimal breeding system. On a pathway to dioecism, such as is discussed by Charlesworth & Charlesworth (1978a), Lloyd (1974a, 1974b, 1975a, 1976), Ross (1970, 1978), Ross & Shaw (1971), Ross & Weir (1976), and Webb (1979), gynodioecious grass is of some evolutionary interest; as a result of occasional but nonpersistent male sterility in many species it is of some interest to plant breeders.

INCOMPATIBILITY

Lundqvist in 1954 demonstrated the genetics of self-compatibility in *Secale cereale*, and in later papers he showed that the system occurred widely enough in the family to be considered the grass or *S-Z* system (Lundqvist, 1955, 1962, 1965, 1969). Work in *Briza*, *Phalaris* and other grasses has been in full agreement (Hayman, 1956; Murray, 1974); in *Lolium* Hayward & Wright (1971) and Spoor (1976) obtained some inconsistent results, but Cornish et al. (1979a) obtained an orthodox fit to the grass system.

Incompatibility in the Gramineae is unique and its characters include: (i) 3-nucleate pollen (Brewbaker, 1957); (ii) dry stigmas (Heslop-Harrison & Shivanna, 1977); (iii) action for the most part, but not exclusively, on the stigmatic surface; (iv) two independent multi-allelic *S* loci (*S* and *Z*) with functional dependence in a complementary and cooperative action such that the presence of an identical specificity, e.g., S_1Z_1 in both the pollen and the stigma, results in incompatibility (Lundqvist, 1975). Most of these characters are those recorded where incompatibility is sporophytically controlled, but incompatibility in the Gramineae is gametophytic. Figures 8 and 9 in de Nettancourt (1977) clearly demonstrate the compatibilities and incompatibilities of the system.

Lundqvist (1975, et praec.) considered that the *S-Z* system had arisen by duplication of a one-locus system. Pandey (1977, 1980), who considers that the complementary incompatibility system is a secondary one derived from the primitive one-locus multiallelic system, accepts duplication of an *S*-gene as one major part of the evolution of the two-loci system. He envisages firstly the breakdown of the original self-incompatibility and the development of self-compatibility. This is followed by the reintroduction of self-incompatibility genes through recurrent inter- or intraspecific hybridization, and after selection against *S* competition and dominance to allow these fundamental characters of this system to evolve, a duplicate, independently acting self-incompatibility locus is acquired. Self-incompatibility has reevolved, though the characteristics of the system are now novel and may be less efficient than the original system. Charlesworth & Charlesworth (1979) consider that the grass system is most likely to have arisen when ". . . a variety of (allelic) specificities is initially present without causing an incompatibility reaction, and that selection acts on loci (other than the *S* locus) which affect the chance that pollen which matches an allele in the stigma-bearing plant will be rejected."

Lundqvist (1975), de Nettancourt (1977), and Pandey (1977) emphasize the benefit of the bifactorial system of the grasses over the monofactorial system common to many other families. Because the number of specificities in a population is the product of the number of segregating alleles in each locus, the two-loci system ". . . confers on the population a reduction of cross-incompatibility between plants and a minimized risk of random loss of members of its valuable pool of incompatibility genes" (Lundqvist, 1975). Recent contributions to the genetics of the two loci are from Charlesworth (1979) and from Cornish et al. (1979b).

The grass incompatibility system prevents fertilization between genotypes identical in incompatibility alleles, and like other incompatibility systems protects

and regenerates itself. Advantages are reflected in recombination and reconstitution; and for the Gramineae if these qualities are desirable, they are achieved by the retention of a versatile, advanced incompatibility system.

This efficient incompatibility system has other attendants. The grasses show what Stebbins (1974) called an extreme adaptation for wind-pollination and cross-fertilization: lodicules controlled by weather; elongation of the stamen filament leading to anthers being presented in a new orientation, pollen quickly shed into the air, abundant, light, easily dispersed; large easily exserted stigmata. Yet, none of these attributes prevents (i) a high level of compatibility between sibs where seed dispersal results in a very narrow distribution, (ii) the mutation self-incompatibility to self-compatibility, (iii) the evolution of the diverse floral array seen in the family.

Pandey (1977) even sees the pseudocompatibility and the high level of sib-compatibility that arise from the two-loci incompatibility system, as extremely advantageous in long-distance dispersal from a single diaspore; both these characters are usually interpreted as the least efficient aspects of the two-loci complementary system. The accidental arrival of a second diaspore from a long distance, and a second accident is as likely as the first, will restore the incompatibility system.

The reevolution of a self-incompatibility system from derived self-compatibility as described by Pandey (1977, 1980) is of very low likelihood if the taxa had long been self-compatible. Added to this, there is no known self-incompatibility system in the grasses that could have had a two-loci complementary system as its progenitor; if such a system were to evolve, it would be of the less efficient one-locus *Tradescantia* type. For those self-compatible grasses where an out-breeding system would be advantageous and which selection might favor, the choice is among various forms of monoecism and dioecism. The proposals of Charlesworth & Charlesworth (1978a, 1978b) for the evolution of these states demand the presence of high levels of self-compatibility; these proposals accord with the potentialities indicated by Pandey (1977, 1980).

Conclusion

Is there an optimal breeding system for the Gramineae? Self-incompatible hermaphrodite flowers in many-flowered spikelets, in inflorescences of many spikelets would seem a very efficient option; such a combination of characters would annually yield a large number of seeds of varied genotype, and no secondary characters would be involved. This state is reached in its fullest expression in the Festuceae, and in some related tribes in the Festucoideae, such as Aveneae, Bromeae, and Hordeeae. Such a conclusion is valid only within the narrow confines of the questions being examined. The conclusion makes no allowance for any other factors preceding seed setting, e.g., floral induction, or consequent upon seed setting, e.g., seed dispersal; it makes no allowance for any ecological considerations, e.g., duration of growing season; it makes no allowance for life-history, e.g., annuals or perennials. And it makes no allowance for the natural distribution of the tribes of grasses on the face of the earth.

The Festucoideae are not especially well known for alternative reproductive systems, self-compatibility excepted; apomixis is known in *Calamagrostis, Hierochloe, Poa,* and very slightly in *Agropyron*; there is very sparse dioecism, and little monoecism, much of it in *Poa.* Members of this subfamily show that, although apparently possessing many of the characters that would seem the most advantageous, other breeding systems have evolved if even only sporadically, or are now the residuum of evolution.

Any analysis leading to the conclusion favoring the festucoids as possessing the most efficient breeding system in the grasses could be a biased one, biased by the overwhelming evidence from temperate grasses. That so many grasses differ from the festucean model reflects the fact that the adaptive values for grasses include more than the requirement of a self-generating incompatibility system, and indicates that one seed in an andromonoecious spathate raceme, or monoecious axillary paniculodium, may well have equal or superior adaptive values in the tropics and subtropics.

The Gramineae, if viewed solely by the array of breeding systems found there, is an advanced family in the Monocotyledonae. Stebbins (1974) found that the grasses are ". . . the climax of flowering-plant evolution . . . ," but his conclusion was logically based on an examination of all the qualities in the family. Bews (1929) was astonished that such an unspecialized system of pollination could be associated with so successful a family.

The grasses show relative conservatism in the arrangement of the flower; in the development of the breeding systems associated with those flowers there is relatively less conservatism, though never flamboyance. The major reproductive systems known in the Plant Kingdom are represented except heterostyly, sporophytic control of incompatibility, and overt insect pollination, though entomophily probably occurs in the tropics.

Although there are some unexpected features of the incompatibility system (Lundqvist, 1954, et seq.), and some unique conditions at pollination (Heslop-Harrison, 1979, 1980), self-incompatibility is basic to the family. For an hermaphroditic, anemophilous, self-incompatible group, optional ways of ensuring seed setting are those leading towards (i) self-compatibility in demanding ecological conditions; (ii) production of abundant pollen to ensure cross-fertilization in competitive genetic conditions; (iii) espousal of apomixis in conditions of polyploidy, and of hybridism. Under self-compatibility as described in (i), initial significant inbreeding depression would be the major disadvantage; for the cross-pollination proposition an excess of flowers that are pollen producers only (andromonoecism) places a low genetic value on ovules and leads to their loss from flowers; and apomixis has always been selected against, resulting in the facultative rather than the obligate form.

There was an early and frequent loss of the incompatibility system without polyploidy as a direct cause, yet self-compatibility is an essential prerequisite only for the development of cleistogamy. Dioecism could evolve from self-compatible progenitors, as could monoecism. For self-compatible grasses an escape is dioecism; monoecism does not guarantee that surcease. Hermaphroditism, alone or in some monoecious combination, sustains most of the world's grasses, and those grasses that are the sustenance of the world.

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COEVOLUTION OF GRASSES AND HERBIVORES

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ABSTRACT

The appearance of fossilized silica bodies derived from the leaf epidermis of grasses and of mammalian fossils having high-crowned teeth was nearly simultaneous in lower to middle Eocene strata of Patagonia, where these fossils are associated with dry land sediments that indicate the presence of savannas containing shrubs and traversed by rivers that provided mesic habitats. In North America, the earliest clearly identified grass fossils are stipoid fruits of lower Miocene age, while the oldest mammals having high-crowned teeth are rhinoceroses of Miocene age. The abundant stipoid fruits known from the Miocene and Pliocene Epochs in the central United States indicate that the earliest Miocene species were quite different from modern counterparts, but that early Pliocene species have modern counterparts in the pampas of South America. During the Pleistocene, stipoid grasses ceased to be dominant elements of North American grasslands, being replaced by grasses belonging to the tribes Chlorideae and Andropogoneae. This change was associated with the appearance of a drier, more continental climate and with the appearance of bison and sheep on the North American plains. The evolutionary significance of these coordinated changes is discussed.

A fundamental tenet of modern evolutionary theory is that, at least with respect to visible morphological and anatomical characteristics, rates of evolution reflect to a large degree rates of change through time in the nature of population-environment interactions (Dobzhansky et al., 1977). Rapid evolution is often associated with successful responses to rapid and complex changes in the environment. The environmental changes that stimulate most strongly rapid evolution involve both the physical and biotic environment. Often the changes in climate and similar physical factors trigger off changes in structure and behavior on the part of those organisms that have the most direct relationships with the external environment, and these in turn affect other organisms of a given community.

An excellent example of rapid evolution as a result of this complex web of physical and organismic changes is the evolution of grasses and the herbivorous mammals that depend upon them. Paleobotanists and vertebrate paleontologists from both North America and South America have now accumulated data that can be synthesized into an account of this coevolution which, though admittedly partial, is nevertheless highly convincing. The very different history of events occurring on these two continents, plus the remarkable synchrony on each continent between the evolution of grasses and mammalian herbivores shows clearly the close interdependence between the evolution of these two very different kinds of organisms.

THE KINDS OF EVIDENCE THAT ARE AVAILABLE

The most important kind of evidence from which the story can be pieced together is provided by the fossil record. Fortunately, this record is remarkably good in both North and South America, including remains of both grasses and mammals. The grass fossils that are the most diagnostic are fruits that clearly belong to the tribe Stipeae. The pioneering monograph of these fruits prepared by Elias (1942) has now been supplemented by more modern and thorough re-

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search on the part of Thomasson (1978a, 1978b, 1979). The remarkable features of these fossils are both their abundance and the details of cellular structure that can be seen in them. Moreover, in contrast to most other fossils of angiosperms, they reveal characters of form that are usually used by systematists dealing with their modern counterparts as diagnostic of species and genera.

Next in importance are fossilized bits of leaf epidermis. To my knowledge, the only definite fossils of this kind are those discovered by Litke (1968) in coal deposits of eastern Germany. In them, cell outlines are perfectly preserved, so that identification to tribe is unquestionable. They show that at least one tribe of the family, the Oryzeae, was already differentiated by the end of the Eocene Epoch.

Of a similar character, but harder to identify, are the much more abundant bits of organic silica known as opalines, that occur in some sediments. These microscopic particles are derived from epidermal cells of grasses that have become fully impregnated with silica. When well preserved, they are diagnostic of subfamilies, as shown by Prat (1932) and others. Most reports of these fossils are from sediments of Pliocene age, but much older examples, some of them dating from the middle or early Eocene, have been reported from Patagonia, South America (Frenguelli, 1930; Teruggi, 1955; Bertoldi de Pomar, 1971, 1972).

The pollen of Poaceae is highly distinctive as to the family, but of little value for the recognition of its subdivisions. It does not become abundant until the Miocene Epoch, when evidence from fruits and epidermal fragments indicates that the family was already fully differentiated. For this reason, palynological fossils are among the least valuable for reconstructing the evolutionary history of the family. Leaves that on the basis of superficial appearance have been assigned to the family and given such generic names as *Poacites* are even less helpful. Recent studies of some of them on the basis of microscopic cellular structure has shown that they belong to other families of monocotyledons (Litke, 1968).

The supreme value of fossils of mammalian herbivores lies in the fact that the parts that are most commonly preserved—teeth and hoofs—are highly diagnostic of both their morphological relationships and their mode of life. High-crowned (hypsodont) teeth having complex patterns of enamel evolved in response to pressures exerted by a diet of hard, siliceous leaves, particularly those of grasses. Long slender legs that terminate in hoofs made up of one or two much enlarged toes evolved in response to rapid running or leaping in country that was at least partly open and free of dense forests. Consequently, hypsodont teeth and well-developed hoofs can be expected to be associated with fossil remains of grasses that are adapted to open country. The frequent presence of this coexistence, or coadaptive syndrome, will become evident from the facts to be presented below.

Direct fossil evidence can be supplemented by indirect evidence of several kinds. Particularly useful is that derived from detailed studies of sediments (Pascual & Odreman, 1971; Andreis, 1972; Spaletti & Mazzoni, 1978). The presence of saline deposits and gypsum in beds that are clearly terrestrial rather than marine in origin indicates at least seasonal drought. Other characteristics, such as deposits resulting from showers of volcanic ash, and the nature of indications of animal activity, such as burrows of worms and nests of scarab beetles, can also be helpful.

Another kind of indirect evidence can be obtained from comparative studies of successions of fossils through time. Because of their high diagnostic value, mammalian fossils are particularly helpful for deciding when a succession represents progressive evolution in situ, and when a change in faunas is due to migration from another region. Although successions of plant fossils are rarely complete enough to lead toward decisions of this kind, an exception is provided by the fruits of Poaceae, tribe Stipeae, that have been uncovered on the plains of the central United States. The combined study of these grass fossils and the mammalian remains associated with them provide the best opportunity for analyzing coevolution of terrestrial plants and animals over a long period of time that exists anywhere in the world.

Indirect evidence can also be obtained from geology, particularly the discipline of plate tectonics, that provides indications of past continental movements. This subject has been carefully reviewed by Raven & Axelrod (1974). Nevertheless, great caution must be used in applying this evidence to problems of plant and animal dispersal. Even with respect to organisms that are least able to be transported over long stretches of ocean, such as mammals, one cannot assume automatically that a land bridge is necessary to transport them from one continent to another. As reviewed by Patterson & Pascual (1968, 1972), a combination of comparative fossil evidence and that related to past continental movements indicates that during the end of the Cretaceous and the beginning of the Tertiary Period, several groups of mammals must have reached South America by migration over water. Since most seeds of angiosperms can be transported over long distances as easily or more easily than can mammals, the entrance of angiosperm groups into South America during the same period by occasional long distance migration can by no means be ruled out.

Finally, modern patterns of geographical distribution can supplement those provided by fossils. These must also be interpreted with caution, and associated with fossil distribution patterns whenever possible. With respect to grasses, the inference is reasonable that the migration of Stipeae, for which a fossil record is available, was accompanied by migrations of grasses belonging to other tribes, which left no record because both their vegetative parts and their seeds are too perishable. Since phylogenies involving polyploidy usually proceed from lower to higher levels (Stebbins, 1971, 1980) inferences about past patterns of distribution can often be obtained by comparing the distribution patterns of diploids and related polyploids (Stebbins, 1947, 1950, 1971).

Relevant Features of Climatic Change and Continental Movements

The record of coevolution between grasses and herbivores spans most of the Tertiary and Quaternary Periods. It begins in southern South America (Patagonia) in the middle of the Eocene Epoch, about 45 million years ago, and continues until the retreat of the glaciers in the post-Pleistocene and the consequent post-glacial xerothermic stage permitted the establishment of open xeric grasslands in the west central part of the United States, plus adjacent Canada and Mexico, less than 10,000 years ago. Climatic and orogenic changes throughout this long period are relevant to the problem.

The story of these changes has been reviewed so many times that it does not need to be repeated here. North and South America underwent a gradual cooling of climate, accompanied by the rise of the western cordillera, that increased habitat diversity, and brought to the central regions of the continents the continental climate that now exists in them, characterized by cold winters and hot summers. Of particular interest, however, are the differences between the two continents in the intensity of these effects. The differences will therefore be reviewed.

In the first place, semiarid conditions, including the appearance of open savannas dotted with widely spaced trees and shrubs, appeared in South America about 20 million years before their appearance in North America. On both continents, the Paleocene Epoch was characterized by continuous forests perhaps interspersed by small enclaves of open country. In the middle of the Eocene, however, evidence from the Mustersan strata in the Province of Chubut, Argentina at 45° south latitude, indicates the presence of widespread savanna conditions, as is described in more detail below. Although direct evidence for the age of these strata is lacking, Marshall et al. (1977) have estimated their age as middle Eocene, about 48 million years old, on the basis of stratigraphic evidence plus a potassium-argon date of 35 million years for a sample from the younger Deseadan formation. At this time, evidence from the fossil record of both plants and animals indicates that central North America was still covered by more or less continuous forests.

Second, the greater land mass of North America caused that continent to respond to the uplift of mountains by acquiring a much greater degree of continentality than that which prevails in South America. This difference, which is evident to anyone who has travelled over the two continents, is clearly shown by comparisons between the different climate diagrams presented by Walter & Lieth (1967). Its relation to the timing of environmental changes is highly important. Equable climates persisted in central and eastern South America long after they had disappeared from corresponding parts of North America. This means that plant species or genera, arriving in South America during the Tertiary Period, had a greater change for persisting in a relatively unchanged condition than did their relatives that remained in North America. In many respects, the present, or rather pre-human conditions prevailing on the pampas of Argentina, Uruguay and southern Brazil during the Miocene and early Pliocene epochs probably resemble more the conditions that prevailed on the Great Plains of North America during the Miocene and early Pliocene epochs than those that prevail there today.

Another important difference is with respect to the biogeographic connections that existed on the two continents. South America was an island continent from the end of the Cretaceous Period until the end of the Tertiary. It received immigrations from other continents only via occasional long distance dispersal, except for a possible closer link with Antarctica. North America, on the other hand, was intermittently connected with Eurasia by land bridges that permitted extensive transmigrations of flora and fauna. Consequently, the early Tertiary mammalian fauna of South America was decidedly unbalanced, being derived from a few accidental introductions (Patterson & Pascual, 1972). Balance was achieved by extensive adaptive radiation from this small number of immigrant stocks. On the other hand, the fauna of North America was constantly receiving immigrants from Eurasia, so that the fauna of the Northern hemisphere was at

all times balanced, and contained several different potential competitors for each new ecological niche that was opened up as a result of environmental change. There is every reason for believing that the same factors produced comparable differences in the evolution of grasses and other angiosperms.

Finally, the two continents were affected very differently by the Pleistocene glaciation. In North America, the Great Plains, that during the Miocene and Pliocene epochs were the scene of coevolution of grasses and mammals, during the Pleistocene were ice covered over the northern part, and farther south became tundra, or coniferous forest (Davis, 1976). On the other hand, glaciation in South America was confined to the high Andes and the southern portion of Patagonia. The extensive grasslands that form the pampas of Argentina, Uruguay and southern Brazil were little affected by this change.

Three factors, therefore, would have contributed to the longer persistence and slower evolution of plains grasses in South America as compared to North America: (1) the longer persistence of equable climates in its temperate regions: (2) the lack of immigration and therefore of new levels of competition during most of the Tertiary Period: and (3) the comparatively mild influence of the Pleistocene glaciation. These factors were, however, balanced by another factor that greatly stimulated both evolution and extinction. This was the massive immigration of northern mammals into South America at the end of the Pliocene Epoch, as a result of the rise of the Panamanian land bridge. As is explained below, this immigration was most probably accompanied by a similar immigration of northern grasses and other angiospermous herbs.

The Succession of Events in the Tertiary History of Grasses and Herbivores

Prior to the Eocene Epoch, no evidence exists for the occurrence either of grasses (Poaceae) or of mammals having teeth adapted to feeding upon them. Primitive ungulates (Condylarths) were widespread during the Paleocene and apparently originated in the Upper Cretaceous (Patterson & Pascual, 1972), but these forms all had low-crowned teeth that lacked complex patterns of enamel. They were almost certainly browsers.

The earliest mammals having hypsodont teeth were the family Archaeohyracidae, of the order Notungulata, that appeared first in the early Eocene strata of Patagonia. They were followed in the middle Eocene by the Notohippidae, belonging to the same order. In the latter family, the evolution of hooflike feet was superficially similar to the much later evolution of hoofs in North American horses. Careful analyses of the land-borne sediments in which these remains were found makes highly probable the conclusion that the animals lived in open savannas, dotted with trees and shrubs, having an aspect not unlike that of the pampas of temperate South America when first visited by Europeans (Andreis, 1972; Spaletti & Mazzoni, 1978). In these strata opalines that were derived from epidermal cells of grass leaves, though scarce, were undoubtedly present (Frenguelli, 1930; Teruggi, 1955). Unfortunately, their state of preservation is such that they cannot be identified as to subfamily or tribe. Contemporary Eocene strata of North America contain fossils of herbivorous mammals, including Condylarths

and primitive ungulates, but these all have characteristics associated with browsing rather than grazing.

The origin of both these Eocene grasses and grazers of temperate South America is in doubt. The Notungulates may have evolved from the more primitive Condylarths that are found abundantly in Paleocene strata, in response to selective pressures produced by the changing habitats. Could the grasses have also evolved from more primitive, forest-loving groups? This hypothesis is certainly plausible, in view of the present distribution of primitive grasses in the forests of tropical South America. This region is a center of diversity not only for bambusoid grasses having relatively low chromosome numbers, (Soderstrom & Calderón, 1974), but also for genera such as *Streptochaeta* and *Anomochloa*, that are either archaic or appear to have diverged in their own unusual direction from primitive ancestors.

One cannot, however, conclude from these facts that the Gramineae as a whole originated in South America. Bambuseae having similar low chromosome numbers exist also in West Africa, and the subfamilies of nonbambusoid grasses that had the largest number of unspecialized characteristics, particularly the Arundinoideae, tribe Danthonieae, are far better developed in Africa than in South America. Furthermore, the isolation of South America during the Eocene would make highly improbable the emigration of Poaceae from that continent to the other continents where they certainly existed during the middle of the Tertiary Period. The existence of the subfamily Oryzoideae in Europe during the Upper Eocene (Litke, 1968) is highly significant in this connnection. Consequently, I believe that Poaceae most probably entered South America from the Old World, possibly Africa, during the Paleocene Epoch or the uppermost Cretaceous. Although Africa and South America were already well separated during this time, islands may well have existed between them in the South Atlantic. These could have served as stepping stones for long distance migration. This hypothesis has been advanced by Raven & Axelrod (1975) for many elements of the South American biota, both flora and fauna.

During the Oligocene, the coevolution of grasses and herbivorous grazers in South America continued along the lines that were begun during the Eocene. Several groups of Notungulates became even more diversified and specialized for life in open savannas. The accompanying evolution of grasses has left no record, except that the scattered presence of opaline siliceous bodies suggests that they also were actively evolving. In North America, the earliest evidence that Poaceae were present comes from the Florissant deposits of uppermost Eocene or earliest Oligocene (MacGinitie, 1953; Beetle, 1958; see Epis & Chapin 1975 for accurate dating). These are fruits of two different kinds, one of them belonging to the tribe Stipeae, and perhaps the genus *Stipa* itself, and the other possibly to the genus *Phalaris*. Both of these genera belong to the subfamily Pooideae, but to different tribes, Stipeae and Phalarideae, respectively. The existence of such genera, that are end branches of different lines of evolution within the subfamily, suggests that the Pooideae were already well differentiated at that time. This conclusion agrees well with the completely modern character of the pooid fragments of epidermis found by Litke (1968) in Miocene coal-bearing strata of Germany.

Both *Stipa* and *Phalaris* most probably reached North America from Eurasia.

The probable origin of subfamily Pooideae ("Festucoideae") in temperate Eurasia has been emphasized by Hartley (1973) on the basis of modern distribution patterns. The two largest genera of the tribe Stipeae, *Stipa* and *Oryzopsis*, both have pronounced centers of diversity in central Asia (Komarov, 1934). The species of (*Phalaris*) are also primarily Eurasian. Consequently, the earliest known grasses that inhabited open savannas in North America appear to have acquired their distinctive characteristics by a course of evolution that took place during the Eocene Epoch in Eurasia.

Even though temperate South America is at present a center of diversity for the tribe Stipeae, it probably was not the center of origin for the tribe. The paleosoils of Eocene and Oligocene age in temperate South America, including those of the temperate pampas where Stipeae are now abundant, have been examined as carefully as have the Miocene deposits of North America. The absence of stipoid fossils from South American deposits is, therefore, as significant as their abundance in North America. Stipoid grasses most probably migrated from North to South America contemporaneously with the ungulates of North American origin, such as camels and horses.

Incredibly rich deposits of stipoid fruits of "seeds" have been found in Miocene and Pliocene deposits of central North America, extending from Nebraska and Kansas west to Colorado, and southward to New Mexico. They provide what is probably the best fossil sequence of herbaceous angiosperms anywhere in the world. Even though the stratigraphic succession, as worked out by Elias and others, has recently been questioned (Thomasson, 1979), a phylogenetic succession of fruit forms can still be recognized. The known sequence begins in the early to middle Miocene with *Berriochloa primaeva* Elias, which apparently has no modern counterpart, and ends in the Lower Pliocene with a series of well-differentiated forms that can be assigned to the modern genera *Stipa*, *Oryzopsis*, *Piptochaetium* and *Nassella*.

Stipoid grasses evolved contemporaneously with two groups of grazing ungulates, horses and pronghorn "antelopes." The Eocene and Oligocene representatives of the horse line that evolved in central North America were small to medium-sized in stature, had low-crowned teeth and feet consisting of three or more digits (Romer, 1966; Simpson, 1951). During the Miocene, successive genera of horses increased considerably in size. At the same time, they radiated adaptively into two different lines. One of them led to *Anchitherium* and *Hypohippus*, which became relatively large, but retained teeth equipped for browsing (Simpson, 1951). In the other, represented in the Miocene by *Merychippus*, adaptation to grazing evolved through the acquisition of teeth having more complex patterns of enamel, accompanied by cement. These horses also ran more firmly on their middle toe and acquired a springing gait more like that of modern horses. In the earlier horses and the *Anchitherium-Hypohippus* line, the hind part of the foot consisted of a flexible pad or cushion, much as in the feet of modern dogs or camels. The presence of this pad prevented the animal from flexing its toes or hoofs, an action of horses that is essential for fast running of a relatively large animal. Consequently, an adaptive change correlated with the altered teeth was the loss of this pad, and the evolution of a springing motion during running, based upon the flexion of the middle toe. *Merychippus* and its descendants became

adapted to more open savannas, that were increasing in extent during the Miocene epoch. The shift in diet was probably a result of selective pressure brought about both by the increased abundance of grasses relative to the foliage of shrubs and trees, and intense competition for the latter from other browsers including tapirs, rhinoceroses, chalicotheres and camels, as well as *Anchitherium*-type horses. The perfection of teeth adapted for grazing most probably coincided with the evolution of firmer, more siliceous leaves on the part of the grasses that grew in the more open areas.

At the end of the Miocene, a second adaptive radiation took place. Three closely related lines of this radiation retained the three-toed hoofs of *Merychippus*, but acquired teeth having higher crowns. The three terminal forms, *Nanippus, Neohipparion* and *Hipparion*, differed from each other in body size and details of tooth structure. Of these, *Nanippus* and *Hipparion* persisted throughout the Pliocene. In the fourth line, represented during the Pliocene by *Pliohippus* and later by modern horses (*Equus*), the changes in teeth were somewhat similar, but those of legs and toes were more profound. The legs became longer and more slender, and the side toes were lost, producing the single large hoof characteristic of modern horses.

A highly significant fact about Pliocene evolution of horses, worked out in detail for the Great Basin by Shotwell (1961), was the contemporaneous and largely sympatric existence of two quite different kinds of horses, *Hipparion* and *Pliohippus*. Shotwell infers that they occupied somewhat different habitats; *Hipparion* living in savannas or parklands containing many trees and shrubs, while *Pliohippus* occupied the more open areas. He suggests that the side toes provided added traction in dodging movements while the animal was escaping from predators in savannas or parkland, while the presence of a single large toe made running in a straight line more efficient for a horse that lived chiefly or entirely in open country. Comparing the distribution throughout the Pliocene of *Hipparion* and *Pliohippus*, Shotwell concludes that the spread of *Pliohippus* at the expense of *Hipparion* coincided closely with spread of open grassland, replacing savanna or parkland. Apparently, the direct response to the increasingly dry climate was with respect to the flora, but that the horses, with little or no further evolution, altered their distribution in response to the change in vegetation. Thomasson, reviewing the change in vegetation and in horse distribution in the Great Plains of the central states, concludes that the same interacting succession of events took place there.

Unfortunately, grass fruits have not been found in deposits younger than early Pliocene, so that the changes in flora during the last five million years cannot be followed. The changes that took place must be inferred from comparisons between the fossil fruits dating from the earliest Pliocene and the composition of the modern floras. These are as follows. In the South American pampas the stipoid genera *Stipa, Nassella* and *Piptochaetium*, not known as fossils, are now abundant and represented by a large number of species. In North America, on the other hand, stipoid grasses are much less abundant than they were during the early Pliocene. The genus *Stipa* is represented chiefly by *S. comata, S. spartea, S. viridula* and *S. robusta*, all of which have fruits that differ considerably from the Pliocene fossils. A fact to be noted is that the first three of these species are

polyploids. The chromosome number of both *S. comata* and *S. spartea* is $2n$ = 44 to 46, depending upon the presence or absence of a small extra pair, perhaps of B-type chromosomes (Stebbins & Love, 1941). That of *S. viridula* is $2n$ = 82 (Johnson & Rogler, 1943). Since the modern fruits of these species are considerably larger than any of the Pliocene fossils, one can suspect that their polyploidy arose during the later Pliocene, Pleistocene, or even more recently.

The other two genera that are known from fossils of Pliocene age, *Nassella* and *Piptochaetium*, are now absent from the central and western grasslands. *Piptochaetium* survives in the arid mountains of the southwest, as well as in the form of two species that are usually placed in the genus *Stipa*, *S. avenacea*, which occurs in rocky woods throughout the eastern United States, and *S. avenacoides*, native to open, savannalike woodlands in Florida. North of temperate South America, *Nassella* is represented only by a few localized species in Mexico and Central America.

The stipoid grasses have been largely replaced in the Great Plains by genera belonging to three completely different tribes; the bluestems (*Andropogon*, s.l.), belonging to the tribe Andropogoneae; switchgrass (*Panicum virgatum*), tribe Paniceae; grama grass (*Bouteloua curtipendula* and *B. gracilis*) and buffalo grass (*Buchloe dactyloides*), the latter two both of the tribe Chlorideae. When and why did this revolutionary change take place?

No definite answer can be given to either of these questions. The answer to the question "when?" is made difficult by the absence of grass fossils dating from the Upper Pliocene and Pleistocene epochs. If, as seems likely, stipoid grasses were associated chiefly with savannas and grasses belonging to other tribes were predominant on open plains, then the gradual restriction of savanna habitats, as can be inferred from the distribution of *Hipparion* and other fossil mammals, must have been associated with a similar decrease in abundance of stipoids, or at least of those species that occur in the early Pliocene deposits. This would mean that by the end of the Pliocene epoch, the genera *Berriochloa*, *Piptochaetium* and *Nassella* had already disappeared from most of the central plains. Nevertheless, they probably persisted in some parts of the area as late as early Pleistocene. This inference is based upon my belief that their invasion of the South American pampas was simultaneous with the transcontinental migration of northern ungulates, particularly horses (Equidae) and Camelidae. This migration is usually dated as immediately following the appearance of the Panamanian land bridge, at the end of the Pliocene or the beginning of the Pleistocene epoch.

At the beginning of the Pleistocene glaciations, therefore, the composition of the grass flora of the central plains was probably already different from that recorded in lower Pliocene deposits. Such a change would be expected as a result of increasing aridity and progressively colder winters, which is evident from the composition of woody floras from throughout the western United States (Axelrod, 1975). Species of the genera *Stipa* and *Oryzopsis* were probably there, as they are today, as well as *Agropyron* and *Elymus*, which probably entered North America from Eurasia during the Pliocene (Stebbins, 1974). Species of the genus *Panicum*, perhaps descendants of the Mio-Pliocene *P. elegans* and relatives of the modern *P. virgatum*, were probably present. Nevertheless, good reasons exist for believing that three of the dominant elements of the modern grass flora,

the bluestems (*Andropogon* or *Schizachyrium*), indian grass (*Sorghastrum*), grama grasses (*Bouteloua*) and buffalo grass (*Buchloe*), were either absent or uncommon. As discussed elsewhere (Stebbins, 1974) the species of these groups that now dominate the plains are polyploids that appear to have close diploid relatives either in the southern United States or in Mexico. The polyploid complexes to which they belong have distribution patterns that suggest youthfulness (Stebbins, 1971). I believe, therefore, that these species are of post-Pleistocene origin.

Throughout the Pliocene epoch, the mammalian herbivores that dominated the Great Plains belonged to the same evolutionary lines that had been evolving there during the Miocene: horses, pronghorn "antelopes" and camels. They were becoming larger, and gave rise to a number of branches off their main evolutionary lines. Nevertheless, their effect upon the plains grasses must have been similar to that exerted by their Miocene ancestors, though perhaps more intense.

The Pleistocene glaciations, plus the profound effects that they exerted on both climate and soil for hundreds of miles south of the ice margin itself, must have altered greatly the central and western grasslands. Immediately south of the ice margin, grasslands were replaced by tundra and spruce forest, even in areas that are now short grass plains, such as north and central Nebraska (Davis, 1976). During drier periods, the accumulation of loess must have altered greatly soil conditions, contributing further to the displacement of floras.

During the Pleistocene epoch, the fauna of herbivores was altered by the arrival of bison and sheep from Eurasia. These animals graze more closely and densely than do horses and pronghorns, which dominated the plains before their arrival. They would be particularly destructive to long-leaved caespitose or bunch grasses, such as most species of *Stipa* and perennial Triticeae. On the other hand, rhizomatous, sod-forming grasses, such as *Bouteloua* and *Buchloe*, would be much more resistant to their grazing pressure.

For these reasons, I believe that the grassland vegetation of the central and western United States, as recorded by the botanists who first visited the area during the nineteenth century, consists of recent plant communities that were put together after the retreat of the last ice sheet. Some of their contemporary species may have arrived or at least spread during comparatively modern times, as a result of burning and other activities on the part of the Indians (Gleason & Cronquist, 1964: 206–208). Coevolution of grasses and herbivores has progressed continuously on the North American grasslands ever since they first appeared as savannalike openings in the forest during the early part of the Tertiary period.

CONCLUSION

In spite of large gaps in the fossil record, available information permits a partial synthesis that reveals close connections between the evolution of large mammalian grazing herbivores and the grasses upon which they fed. This coevolution began during the Eocene Epoch, 45 to 55 million years ago, and has continued up to the present. Further research studies, conducted in a variety of disciplines, will surely fill in and amplify the picture. Paleosoils need to be examined more carefully, with particular reference to the possible occurrence in

them of opaline silica bodies derived from grass leaves. Whenever these are well enough preserved, they could be examined by agrostologists who might be able to determine at least approximately their systematic affinities. More information is needed about the stipoid fruits found in the Great Plains area, particularly their total distribution in both space and time. At the same time, careful morphological comparisons between the fruits of species belonging to modern stipoid genera will help greatly in the classification of the fossil forms, and for estimating the amounts of difference between them. A synopsis of morphological and histological characteristics of stipoid fruits on a worldwide basis will be necessary for interpreting such comparisons. Cytogenetic and biochemical comparisons of different modern species and genera will be a necessary prelude to the interpretation of evolutionary relationships.

In addition, the effects of grazing animals upon the species composition need to be better understood. Research workers in the discipline of range management have conducted many experiments to show that different intensities of grazing affect greatly the species composition of range lands. In addition, trampling by hoofs of the grazers exerts additional effects, particularly during wet seasons. This kind of damage is quite different depending upon the kinds of hoofs that the different species of grazers possess. Other factors are the different sizes of the flocks and herds that are characteristic of different species, and the tendency of some of them to travel long distances, while others remain for relatively long periods of time in the same area. I am not aware of any careful investigations even of the comparative effect on range lands of different kinds of modern domestic animals, such as horses and cattle, although ranchers and range specialists are well aware of the existence of differences, and anecdotal accounts of them are numerous. In this entire field, the opportunities for collaborative research are very great. They can be directed toward a highly valuable aim: interpreting the evolution of two of the world's major food resources—grasslands and grazing animals. Mankind has depended upon them for his existence ever since our remote ancestors ventured onto the savannas and began a new mode of existence.

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GRASSES AND THE CULTURE HISTORY OF MAN

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Abstract

The beginnings of plant and animal husbandry are lost in antiquity. It is not possible to determine from the available archaeological record when plant domestication was initiated. Changes in phenotype, however, known to be associated with cereal species under domestication, and preserved in the archaeological record indicate that growing crops was an established way of life some 10,000 years ago. There are four major domesticated cereal complexes. Three evolved in the Old World and one in the New World. Wheat, barley, rye and oats are Near Eastern cereals, and spread across Eurasia early during the history of agriculture. Rice is the principal cereal of South Asia, sorghum and pearl millet the major cereals of the African savanna, and maize is a domesticate of Mesoamerica. Why the shift from hunter-gatherer to settled agriculturist occurred during the culture history of man is not known. Food production may have been initiated when man was faced with a gradual reduction in productivity of effort required to maintain accepted standards of living, traditional group size, and social organization. Once initiated, population pressures in particular will tend to demand agriculture. Hunter-gatherers live in equilibrium with the environment and have little lasting effects on nature. Farming, by its very nature, destroys the natural environment. Habitats are permanently altered, and a return to hunting and food gathering becomes impossible. Survival of civilized man has become absolutely dependent on cereal agriculture. Overpopulation, depletion of resources, planetary pollution, and the social ills of cities are penalties we have to pay for the pleasures of an abundant and stable food supply.

Grasses have been playing a principal role in shaping the culture history of man every since he became sapient. They are basic to human life. The staple food of the great majority of mankind comes from grasses and they provide food for the grazing animals from which man derives most of his protein. The Gramineae is a relatively young but successful family. It includes an estimated 600 genera and 8,000 species that are widely distributed across the world. Grasses occur on all continents, including Antarctica, and are absent only from regions that are too barren or too cold to support the growth of flowering plants. The fossil record of grasses is meager, but there is good evidence to suggest that they emerged as a distinct family during late Cretaceous times when the flowering plants were spreading throughout the world. By early Miocene grasslands probably were assuming a prominent place in the earth's vegetation, and it is estimated that at present almost one-quarter of the world's plant cover is composed of grass (Barnard, 1969).

The evolution of the family has been strongly influenced by herbivorous mammals. Early ungulates were probably browsing, rather than grazing animals. Nonruminant kinds of Artiodactyla appear in the fossil record from the early Tertiary. Ruminant forms, particularly the Bovinae, arose during the Miocene and have coevolved with grasses ever since. The transverse intercalary growth zone in leaves and above culm nodes, the short internodes of aerial stems of annual grasses, and the tufted habit of perennial grasses during vegetative growth, are adaptations to withstand grazing.

Man appeared on the scene well after the Gramineae and grazing ungulates became widely dispersed. Hominid evolution dates back to the Pliocene, but the

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genus *Homo* appears in the fossil record only since the Pleistocene, and our own species is probably less than 100,000 years old (Isaac & Leakey, 1979). Man started as a hunter and gatherer of plants for food. He competed with animals for the available supply of plant food, and hunted some of these same animals to satisfy his craving for meat. Gradually man learned how to control the food resources in the areas where he lived. Selected animals were protected from their natural enemies, and populations of favored food plants were increased through planting. Plant and animal domestications were initiated, and man started on a path of rapid social evolution.

THE DOMESTICATION PROCESS

The beginnings of domestication are lost in antiquity. It is not possible to determine from the available archaeological record when plant or animal husbandry was first practiced. But, changes in phenotype, known to be associated with particular plant and animal species under domestication and preserved in the archaeological record, indicate that growing crops and herding animals were established ways of life some 10,000 years ago (Higgs, 1972).

The transition from hunting-gathering to plant and animal husbandry occurred in different ways in different parts of the world. Different plant and animal species were domesticated at different times and places across the range of their intensive exploitation by man. Full pastoral nomadism is practiced only in the Old World, and only in areas where growing crops is impossible or totally unreliable as a constant source of food. In the wet tropics and high Andes of South America where grasses are not abundant, cultivation of tubers made settled agriculture possible. On the plains of Africa and Eurasia, and on the highlands of Mesoamerica, grass cultivation provided the staple food for a sedentary way of life.

Domesticated plants depend on man for suitable habitats. This dependence on man-disturbed habitats came about through selection pressures associated with harvesting and sowing (deWet & Harlan, 1975). Weeds are similarly adapted to permanently man-disturbed habitats. The major difference is that weeds are usually spontaneous in this habitat while domesticated taxa depend on man for propagation. The ecological boundaries between the wild, weed and domesticated classes of plants are poorly defined. Wild plants may be aggressive natural colonizers and they are consequently weedy. Weeds may be protected, and wild plants may be cultivated as sources of food. Animal fonio, *Brachiaria deflexa* (Schumach.) C. E. Hubbard is collected in West Africa as a wild cereal. On the Fouta-Djalon highlands of Guinea it is a cultivated cereal (Portères, 1951), and in Angola the species aggressively invades cultivated fields where it is often protected and harvested as a crop (deWet, 1977). Domesticated species may behave as weeds when they have not completely lost the ability of natural seed dispersal. True fonio, *Digitaria exilis* (Kippist) Stapf is widely cultivated in West Africa (Portères, 1955). Its wild progenitor is not not known. But, the cultigen commonly escapes and occurs as a weed in the fields of other crops, where it is often harvested.

Cultivated cereal species are annuals, and their closest wild relatives are aggressive annual colonizers of disturbed habitats. The only exception is *Bromus mango* Desv. (mango). This biannual was cultivated in Chiloé province of central

Chile, until the eighteenth century, when it was replaced by the introduced Old World cereals wheat and barley (Gay, 1865; Molina, 1782; Cruz, 1972). Today *B. mango* is known only as a wild plant, distributed in Central Chile and adjacent Argentina (Parodi & Hernández, 1964).

Colonizing ability is essential in domestication. Propagation by man of selected genotypes, however, constitutes domestication. Sowing of seeds harvested from a planted population results in loss of seed dormancy, an increase in seedling vigor, and eventually the inability of the cultigen to successfully invade natural habitats (deWet, 1975, 1979). Phenotypic traits associated with sowing of annual seed crops are uniform population maturity, and commonly also an increase in fruit size. Harvesting in association with sowing leads to a reduction in natural seed dispersal ability, and uniform individual plant maturity (Harlan et al., 1973). Phenotypic characteristics associated with harvesting are usually persistence of spikelets or florets on the inflorescence after maturity, and either reduction of inflorescence-bearing culms or synchronized tillering. Fully domesticated cereal species depend on man for a suitable habitat as well as seed dispersal. The domestication process continues as long as the cereal is harvested and sown in successive generations.

Selection pressures associated with harvesting and sowing are commonly superimposed on pressures induced by man in selecting for traits to satisfy his fancies. This leads to rapid evolution under domestication. Genetic drift, selection, and isolation allow for phenotypically different kinds of a domesticated species to be grown by different groups of people for the same or different uses. Cultivated grain sorghum, *Sorghum bicolor* (L.) Moench, as an example, is widely grown in Africa and Asia, morphologically variable, and frequently classified into 28 species with 165 botanical varieties and several hundred recognized phenotypes (Snowden, 1936). Genetically, these taxa are conspecific and represent little more than selections that are being maintained by man to suit his fancies and needs (deWet, 1978). Phenotypic changes associated with cereal domestication are often grotesque. The spike of wild pearl millet, *Pennisetum americanum* (L.) Leeke is at most 10 cm long (Brunken, 1977), while some cultivars have spikes over one meter long (Brunken et al., 1977). Even more spectacular are the differences that distinguish maize (*Zea mays* L.) from its closest wild relative *Z. mays* subsp. *mexicana* (Schrad.) Iltis (teosinte).

Maize and teosinte are genetically conspecific, and evidence presented by Beadle (1977) suggests that teosinte is wild maize. These two taxa differ conspicuously from one another in four basic characteristics of the female inflorescence. First, the inflorescence is distichous in teosinte and polystichous in maize. Second, female spikelets are solitary at a rachis node in teosinte and paired in maize. Third, female spikelets of teosinte are individually sunken into indurated cavities on the rachis, each of which is closed by an indurated outer glume to form a fruitcase. In maize the paired spikelets are located in shallow, more or less indurated cupules. Fourth, fruitcases disarticulate at maturity in teosinte but cupules are persistent in maize. These opposing traits are not simple genetic alternatives (Galinat, 1975). Intermediate expressions of tunicate alleles determine induration, recessive alleles of a complex genetic system restores fertility to the rudimentary spikelet of a female pair, and recessive alleles of at least two

genes change the distichous spike of teosinte into the polystichous ear of maize (deWet, 1979).

Phenotypic changes associated with domestication are those selectively favored by man. The three principal innovations of cereal domestication, loss of natural seed dispersal ability, uniform population maturity, and uniform individual plant maturity facilitate harvesting, and increase the percentage of harvestable seed. Phenotypic changes characteristic of individual cereal species under domestication further increase yield, enhance threshing, or are designed to suit the fancies of the cultivator. Increase in inflorescence size commonly accompanies a shift from wild to domesticated. Cultivated maize from the Coxcatlán culture phase in the Tehuacán Valley of Mexico had less than 100 kernels per ear. Less than two millennia later kernel number had increased to over 600 per ear.

Domesticated Cereals

The principal use of grass by man is as cereals. Grasses are also highly valued as feed for livestock, and serve man in many other ways. Landscaping the habitat we live and play in is hardly complete without a lawn. There are turf grasses selected for house lawns, golf courses, parks, and sport fields. Grasses are also planted as ornamentals. No tropical garden is complete without a clump of bamboo, and *Cortaderia selloana* (Schult.) Ashers. & Graebn. (pampas) and *Miscanthus sinensis* Anderss. (eulalia) are popular lawn ornamentals in warm and temperate regions. Grasses provide us with food other than cereal grains. Sugar is extracted from the stems of domesticated *Saccharum officinarum* L. (sugar cane). In the Far East *Zizania latifolia* Turcz. (water rice) is grown as a vegetable. Fungus infests the lower leafbases and the swollen stems are eaten. The young shoots of *Setaria palmifolia* (Koen.) Stapf (jungle rice) are eaten in New Guinea, and the well-known bamboo shoots of commerce are harvested from species of *Bambusa*, *Dendrocalamus*, and *Phyllostachys*. Grasses are also used as fuel, timber, roofing material, and as material from which paper, mats, and containers are made. Two species, *Cymbopogon citratus* (DC. ex Nees) Stapf (lemon grass) and *Vetiveria zizanioides* (L.) Nash (vetiver), are commercially grown for their essential oils that are used in the perfume and pharmaceutical industries.

Grasses serve man in many ways. But, it is their use as cereals that help shape his culture history. The caryopses of most grasses are edible, and at least 300 species are known to be harvested in the wild as cereals. Among these, 35 species belonging to 20 genera are, or were at one time grown as cereals (deWet, 1979). Brittle grass, *Setaria geniculata* (Lam.) Beauv., is known as a cultivated cereal only in an archaeological context from Mexico (Callen, 1965, 1967). Canary grass, *Phalaris canariensis* L., is grown as a food for caged birds rather than as food for man. American wild rice, *Zizania aquatica* L., has been harvested commercially in the wild for centuries, but it is only during the last decade that this cereal has been successfully cultivated (deWet & Oelke, 1978). Ethiopian oats, *Avena abyssinica* Hochst., is not consciously sown but is accidentally planted and harvested with other cereals. It is an obligate weed that has lost the ability of natural seed dispersal (Rajhathy & Thomas, 1974). The biannual *Bromus mango* (mango) was cultivated in central Chile until the eighteenth century, when it was replaced

by wheat and barley. The remaining 30 cereal species are still cultivated, although several of them as minor crops. The major cereals are wheat (*Triticum* spp.), rice (*Oryza sativa* L.), maize (*Zea mays*), sorghum (*Sorghum bicolor*), and pearl millet (*Pennisetum americanum*) in order of their importance as human food. It is estimated that in 1976 some 413 metric tons of wheat, 344 metric tons of rice, and 335 metric tons of maize were produced by the world's cereal farmers.

There are four major domesticated cereal complexes, each with a distinct geographic region of origin (Harlan, 1976). Three complexes evolved in the Old World and one in the New World. The small grains developed in the Near East, with wheat eventually becoming dominant across Eurasia, except for South Asia where rice is the principal cereal. The African savanna provided the world with sorghum and pearl millet, and maize is a domesticate of the highlands of Mesoamerica. The archaeological record suggests that southwestern Asia is the oldest region of cereal domestication, and that the knowledge of agriculture may have spread from here across the Old World and eventually to the New World (Carter, 1977). It is doubtful, however, that cereal agriculture evolved only once. Near Eastern cereals did become widespread across temperate Eurasia and Mediterranean Africa soon after they became domesticated. But, there is no evidence to suggest that the cereal complexes in South Asia, the African savanna, or Mesoamerica were not independently domesticated.

NEAR EASTERN COMPLEX

Three species of wheat, *Triticum monococcum* L. (einkorn), *T. turgidum* L. (emmer) and *T.* × *aestivum* L. (bread wheat), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.) and rye (*Secale cereale* L.) are Near Eastern cereal domesticates. The Natufian of Palestine is the first known culture in the Near East that was equipped to extensively harvest and process small grains (Redman, 1977). Common tools used by the Natufian include grinding stones, stone mortars, and sickles with sheen on their stone blades. Extensive harvesting of cereals demand some kind of sickle, and since the florets of wild wheats and barley are tightly enclosed by glumes, processing is necessary to thresh the grain free.

Remains of wild barley and wild einkorn appear in the archaeological record at Tell Mureybit (Syria) dating back to between 10,050 and 9542 B.P. (Renfrew, 1969). This probably is the period of initial cereal cultivation in the Near East. Loss of natural seed dispersal ability is commonly accepted as indicating domestication of cereals in an archaeological context. However, cereals may have been cultivated for many generations before this domesticated phenotype became established. Domesticated wheat and barley, totally dependent on man for seed dispersal, appear in the archaeological records between 9500 and 8500 B.P. from numerous occupation sites (Harlan, 1977) extending from Turkey to southwestern Syria and Palestine. The practice of growing wheat and barley reached Greece by 8000 B.P., and during the next 2,000 years spread along the valleys of the Danube and Rhine to the Netherlands, and along the Mediterranean to France. Bread wheat, a strictly domesticated taxon, appears around 8000 B.P. in such scattered settlements as Knossos in Greece, Hacilar and Çatal Hüyük in Turkey, Tel Ramad in Palestine, and Tepe Sabz in Iraq (Renfrew, 1973).

Domesticated oats and rye are rare or absent among archaeological plant

remains dating back more than 7,000 years, although wild oats in particular seems to have been commonly harvested for at least 1,000 years before the species became domesticated. Harlan (1977) suggests that these two cereals were added to the Near Eastern complex as secondary crops. They invaded cultivated fields as weeds, were harvested, and eventually became domesticated. Rye is wild in Anatolia and Transcaucasia, and Evans (1976) proposes that the weed race evolved after the spread of cereal cultivation into these regions. When or where rye was first cultivated is not known. Oat is wild in the Mediterranean Basin and widespread in the Near East (Baum, 1977). Cultivated oat is reported from Greece by the late eighth millennium B.P., but the crop only became important some five millennia later and then in Central Europe (Holden, 1976).

There is no evidence for an incipient food production period in Europe before the introduction of domesticated Near Eastern cereals (Waterbolk, 1968). Lake-dwelling settlements such as at Niederwil in northeastern Switzerland, dating back to around 3700–3625 B.C., are characterized by fully domesticated barley and bread wheat, and *Chenopodium album* L., a species probably harvested in the wild as a pseudocereal (vanZeist & Casparie, 1974). Two other cereals, *Panicum miliaceum* L. (proso millet) and *Setaria italica* (L.) Beauv. (foxtail millet) occur in Swiss Lake Dwelling sites (Neuweiler, 1946). Wild foxtail millet occurs across Eurasia, but wild proso millet is known only from Central Asia (deWet et al., 1979; Kitagawa, 1979). It is possible that foxtail millet was independently domesticated in Europe and the Far East, but it seems likely that *Panicum* was introduced to Europe as a domesticated cereal (Werth, 1937). A single cereal, *Avena strigosa* Schrebn. (sand oats) is a truly European domesticate. Wild sand oats occurs in the western Mediterranean region and was probably domesticated as a secondary crop in Iberia. By the end of the prehistoric period, settled farming based on plant and animal husbandry, was an established way of life in Europe (Waterbolk, 1968).

The spread of wheat and barley east into the Indus valley and into China was later than west into Europe. They became important cereals during the Harappa-Mohenjo Daro period between 2500 and 1700 B.C. (Vishnu-Mittre, 1968; Allchin, 1969), and along the lower Indus Valley at Chirand between 2500 and 1800 B.C. (Vishnu-Mittre, 1974). These cereals did not reach China until about 3500 B.P. (Ho, 1969).

Cereals were not the only field crops domesticated in the Near East. Almost as important as cereals are peas, *Pisum sativum* L. (Waines, 1975), broad beans, *Vicia faba* L. (Landizinsky, 1975; Zohary, 1977) and lentils, *Lens culinaris* L. (Ladinzinsky, 1979). These pulses appear in the archaeological record of the Near East as early as cereals. They spread with the cereals across temperate Eurasia, and together made possible the early civilizations of Mesopotamia, Egypt, Greece, Rome, and Europe.

ASIAN COMPLEX

Rice, *Oryza sativa* L., is the principal cereal of South and East Asia. Minor cereals belonging to the Asian complex are *Coix lacryma-jobi* L. (jobs tears) and *Digitaria cruciata* (Nees) A. Camus (raishan) from Assam, *Echinochloa colona* (L.) Link (shama), *Brachiaria ramosa* (L.) Stapf (anda horra) and *Panicum su-*

matrense Roth. ex Roem. & Schult. (sawan) from South India, *Paspalum scrobiculatum* L. (khodo millet) and *Setaria glauca* (L.) Beauv. (korali) from Central India, *Echinochloa frumentacea* (Roxb.) Link. (Japanese millet) from the Far East, and *Digitaria sanguinalis* (L.) Scop. (manna) from Kashir. Manna was also widely collected as a wild cereal in southern Europe until historical times. It is known to be an important cultivated cereal only in Kashmir and the Caucasus. Proso millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*) are the only known Asiatic cereals that were grown in Europe during prehistoric times.

The oldest known cereal agriculture in India was practiced by the Harrapans from the Punjab and the Indus Valley. They were growing wheat, barley, and sorghum by 4500 B.P. (Vishnu-Mittre, 1977). These are introduced cereals, wheat and barley from the Near East and sorghum from Africa. Indigenous rice was added to this complex during the late fifth millennium B.P., and other native cereals were locally domesticated during the Indian Bronze age (3700–3000 B.P.) or later. It is also during the Bronze age that African *Eleusine coracana* (L.) Gaertn. (finger millet) was introduced to South India.

The oldest known Asiatic cereals are rice (*Oryza sativa*), proso millet (*Panicum miliaceum*), and foxtail millet (*Setaria italica*). The two millets are ancient cereals from across Eurasia. They were grown in Central Europe some five millennia ago (Heer, 1886) and were widespread in Yang-shao sites from southern Shensi and Shansi provinces in China dating back at least six millennia (Ho, 1977). Wild foxtail millet occurs across temperate Eurasia and could have been independently domesticated in Europe and China (deWet et al., 1979). Wild *Panicum miliaceum* is known only from Central Asia (Kitagawa, 1937, 1979), and proso millet seems to be truly a Chinese domesticate. If this is true, the presence of proso millet in Europe by 5000 B.P., and possibly in Greece by 8000 B.P. (Hopf, 1962), is surprising. In Europe this millet is commonly associated with wheat and barley. These Near Eastern cereals, however, did not reach China until 3500 B.P. (Ho, 1969). It seems possible that wild *Panicum miliaceum* is or was at one time more widely distributed than is presently known, and as is true of foxtail millet, was taken into cultivation independently in Europe and Asia.

Rice first occurs in the archaeological record of China around 5700 B.P., but outside the assumed Neolithic nuclear area of plant domestication (Ho, 1977). It appears as a cereal in India more than a millennium later. Rice is known from around 4300 B.P. in Harappan sites from Rangpur and is widespread along the lower Indus Valley and southern India about 1,000 years later (Vishnu-Mittre, 1977). Solheim (1971) reports that rice impressions, dating back to around 5000 B.P., are present on pottery from Non Nok Tha in Thailand. It is not possible to determine whether these impressions are of wild or cultivated rice. Wild *Oryza sativa* is native across South Asia (Oka, 1974).

The practice of cereal cultivation was probably introduced to northwestern India from the Near East, and from here or perhaps Africa to southern India some 5,000 years ago. Gorman (1977) proposes that rice was domesticated, together with several rootcrops, in southeastern Asia, and suggests that the initial domestication dates back some nine millennia. Chin (1971), however, concludes that rice farming dates from around 5500 B.P. at Non Nok Tha and Ban Chiang in Thailand, essentially the same date that is suggested by Ho (1977) for rice

cultivation in China. Chang (1976) suggests that rice was first cultivated in ancient India, and that the wide dispersal of this cultigen from this nuclear area led to the formation of three ecogeographic races, indica, sinica, and javanica. It seems equally likely, however, that rice was independently taken into cultivation in at least these three general regions, and that this noncentric (Harlan, 1971) domestication of rice allowed for the development of ecogeographic complexes.

Rice is the principal cereal in South Asia. The other Asiatic cereals are important in more localized regions. Proso millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*) are extensively grown in Central Asia and India. Jobs tears (*Coix lacryma-jobi*) is cultivated in Assam and adjacent Burma, and the Philippines (Arora, 1977). Domesticated races of *Coix* from these two regions are distinctly different, and this crop may have been independently domesticated in northeastern India and the Philippines. Raishan (*Digitaria cruciata*) seems to be an endemic, and possible recent crop of the Khasi hills in Assam (Singh & Arora, 1972). Japanese millet (*Echinochloa frumentacea*) and the Indian shama (*E. colona*) may represent complexes of the same cereal species (Yabuno, 1966). Khodo millet (*Paspalum scrobiculatum*) has been widely grown across the Indian plains at least since the beginning of the Indian Bronze age (Kajale, 1977). *Setaria glauca* (korali) is a Kharif crop in central India, and *Brahiaria ramosa* (anda korra) is little more than an encouraged weed in South India.

As in the Near East, pulses played an important part in the history of agriculture in South Asia and the Far East. The soybean, *Glycine max* (L.) Merr., is an early domesticate from China (Hymowitz & Newell, 1977). Chickpea, *Cicer arientum* L., black gram, *Vigna mungo* (L.) Hepper, pigeon pea, *Cajanus cajan* (L.) Hutch., are native crops of South Asia (Ladizinsky & Adler, 1976; Dana, 1976). The winged-bean, *Psophocarpus tetragonolobus* (L.) DC., is extensively grown in the tropics of Southeast Asia (Hymowitz & Boyd, 1977), and the mung bean, *Vigna radiata* (L.) Wikz., is important across the Orient for its nutritious seeds, edible pods, and young sprouts.

AFRICAN COMPLEX

Cereals grown during prehistoric times in Africa north of the Sahara are typically Near Eastern in origin. Wheat and barley reached the lower Nile Valley by the middle of the seventh millennium B.P. (Wendorf & Schild, 1976) and were staple food crops of ancient Egypt (Wönig, 1886). This is not surprising. North Africa has a Mediterranean climate, and the Nile Valley floods during summer when crops from the African savanna can be grown (deWet & Huckabay, 1967). Near Eastern cereals reached the highlands of Ethiopia, probably not later than the beginning of the Christian era. But, here they were grown together with native African cereals.

The West African savanna and East African highlands produced a cereal agriculture independent from that of the Near East. Native African domesticated cereals include *Pennisetum americanum* (pearl millet) from the Sahel, *Eleusine coracana* (finger millet) and *Eragrostis tef* (Zucc.) Trotter (tef) from the highlands of Ethiopia, and *Brachiaria deflexa* (animal fonio), *Digitaria exilis* (fonio), *D. iburua* Stapf (black fonio), *Oryza glaberrima* Steud. (African rice), and *Sorghum bicolor* (sorghum) from the savanna of western Africa.

The antiquity of native cereal cultivation in Africa is not known. Archaeological remains of finger millet from Ethiopia are estimated to date back five millennia (Hilu et al., 1979). This archaeological race of *Eleusine coracana* has lost the ability of natural seed dispersal, and cereal agriculture in Ethiopia must be substantially older. Wild *Eleusine coracana* is distributed across the highlands of East Africa, but this cereal was probably domesticated in Ethiopia (Hilu & deWet, 1976). Finger millet reached South India around 3500 B.P. (Vishnu-Mittre, 1977). Remains of pearl millet dating back to the third millennium B.P. were uncovered at a lake edge settlement in Mauritania (Munson, 1976). A sequence from gathering wild grasses to growing pearl millet is obvious in this settlement. However, it is unlikely that *Pennisetum americanum* was domesticated at the western edge of the Sahel. Wild pearl millet occurs in the central Sahel and highlands of the central Sahara, the region where this cereal was probably first cultivated (Brunken et al., 1977). Pearl millet was introduced to India and became widely cultivated in semiarid parts of South Asia more or less at the same time as its probable spread across the arid savanna of Africa (Vishnu-Mittre, 1969, 1971). The known archaeological record of sorghum, the most important native cereal, dates back in Africa for only two millennia (Connah, 1967; Clark & Stemler, 1975). But, it was an important crop in India as early as three millennia ago (Vishnu-Mittre, 1974). It is, however, an African rather than Indian cereal domesticate (deWet & Harlan, 1971). Wild *Sorghum bicolor* extends across the African savanna and is commonly harvested as a cereal (deWet, 1978).

Archaeological evidence of early cultivation of other native African cereals are almost completely lacking. The minor African cereals remain more or less endemic to the regions of their probable first cultivation. Wild *Eragrostis pilosa* (L.) P. Beauv., the probable wild ancestor of tef, is widely distributed and extensively harvested in East Africa (Barth, 1821–1865), but tef is grown as a cereal only on the Ethiopian highlands. Animal fonio is an endemic crop of the Fouta-Djalon in Guinea, while true fonio, black fonio, and African rice are grown as cereals only in the West African savanna (deWet, 1977). African rice is primarily a crop of the Niger delta. It never became a major crop in the wet forest east of the Bandama river. Here the principal food is indigenous yams (Baker, 1962).

The paleontological record shows that the Sahara was substantially wetter some 8,000 years ago than it is now, and it is known that around 7000 B.P. people with cattle, sheep and goats were camping along edges of shallow lakes and were probably harvesting wild cereals in areas that are now desert (Clark, 1976). During the next several millennia the Sahara became progressively drier, and by 4000 B.P. the desert extended across most of North Africa. It was probably these nomadic herdsmen, who migrated south into the present savanna, that eventually domesticated the wild cereals they used to harvest. Pearl millet and sorghum are the principal and possibly oldest domesticated cereals of the African savanna. They, together with cultivated indigenous yams and the pulses, *Voandzeia subterranea* (L.) Thauars. (bambara groundnut) and *Vigna ungulata* (L.) Walp (cow pea), made a settled way of life possible. These early farmers made possible cultures that eventually produced the magnificant terracotta and bronzes of Benin around the beginning of the Christian era (Shaw, 1976). Sorghum, pennisetum, cow pea, and the bambara groundnut spread east and south along the savanna,

and they together with finger millet and *Dolichos lablab* L. (an East African pulse) fed the iron age cultures that flourished across southern Africa until the eighteenth century (Fagan, 1967; Robinson, 1966; Summers, 1958).

NEW WORLD COMPLEX

Five cereal species were domesticated in the New World. Brittle grass, *Setaria geniculata* (Lam.) Beauv., was extensively harvested in northwestern Mexico and on the Mexican Central Plateau during prehistoric times (Callen, 1965). This species constituted an important part of the diet of the inhabitants of El Riego cave in Tamaulipas some 7,000 years ago. What is of interest, is that the grains of this cereal steadily increased in size during the 2,000 years it was used as a food, suggesting to Callen (1967) that it must have been cultivated. It was eventually abandoned as a cereal after the introduction of maize to the region and is not known to have been grown during historical times.

Sauwi (*Panicum sonorum* Beal) is an endemic cultivated cereal of the Warihio Indians in southwestern Chihuahua (Gentry, 1942). It is grown among maize, harvested, and the grains are ground into flour and either mixed with milk to produce a drink, or mixed with maize flour to make pinole. Wild *Panicum sonorum* extends from southern Arizona to Honduras. The cultivated race retains the ability of natural seed dispersal. Escaped cultivated kinds, recognized by grains that are larger than those of wild races, are widespread around Alamos in Sonora, and around archaeological ruins in Nyarit and Jalisco, suggesting that sauwi may have been more widely cultivated before the introduction of corn to northeastern Mexico. It is surprising that Father Kino (1684–1685), a missionary and early explorer of northwestern Mexico did not mention this native millet in his writings. Today the species is valued more as a fodder for livestock than as a cereal grain.

Mango (*Bromus mango*) is the only known domesticated cereal that is not an annual. Claudio Gay (1865) was one of a few South American botanists who actually saw this cereal in relatively extensive cultivation. Gay writes that before the conquest, the people of central Chile made a kind of bread without yeast that they called covque, and that this bread was made from a native cereal known as mango. He visited central Chile in 1837 and found mango growing in two fields in the department of Castro. The species is biannual. At the time of his visit to this part of Chile, livestock were allowed to graze on the fields during the first season of growth. Plants were protected from livestock the next year and produced a cereal crop in the fall. Mango was harvested, threshed, and the grain was ground into flour that was used to make bread or chicha. Bread and chicha made from mango were reported to be inferior to that made from the wheat and apples that were extensively grown around Castro by the early nineteenth century.

Gay (1865) mentions a possible second cereal that used to be grown in Chile. It resembled barley, except that the grains were smaller, and it was harvested while the plants were green to prevent the inflorescence from shattering. Laet (1633) describes a cereal called teca, similar to barley, with stems like oats and grains a little smaller than those of rye. Whether teca is the second cereal described by Gay is impossible to ascertain with certainty (Parodi & Hernández,

1964). Later, Molina (1782) talks about two native cereals in Chile, "el Magu," a species of rye, and "la Tuca," a kind of barley. He unfortunately saw neither of these cereals in cultivation. They were already replaced by wheat and barley when his natural history of Chile was written. Ball (1884) reports that the Araucano Indians of Bahia Blanca in Argentina use *Bromus unioloides* H.B.K. (*B. catharticus* Vahl) as a wild cereal. It is possible that this wild cereal represents the teca of Laet (1633) and tuca of Molina (1782).

The only New World cereal of present day importance is *Zea mays* (maize). It was domesticated in Mesoamerica, became widely distributed across the New World by the time of conquest by Europeans, and has since been dispersed across all tropical and warm temperate farming regions of the Old World. Wherever it is adapted, maize is replacing native African and Asiatic cereals except for rice.

Maize is unique in female inflorescence morphology among grasses. The paired female spikelets are arranged in more or less indurated cupules along and around a central rachis in usually eight or more rows. The closest wild relative of maize, *Z. mays* subsp. *mexicana* (teosinte) has a distichous female inflorescence. The oldest indisputable maize known in the archaeological record comes from the Coxcatlán culture phase of the Tehuacán Valley in Mexico (Mangelsdorf, MacNeish & Galinat, 1967a). This maize dates back some 7,000 years and is assumed to be wild maize by Mangelsdorf and his coworkers (Mangelsdorf, 1974). Beadle (1977) points out, however, that this maize lacks the ability of natural seed dispersal and must have been cultivated.

The antiquity of cereal agriculture in the New World is not known. MacNeish (1971) suggests that Barranca horticulture started in Tehuacán Valley between 7000 and 5000 B.C., and Niederberger (1979) points out that fully sedentary communities existed in the Basin of Mexico at least since the sixth millennium B.C. Be that as it may, maize was grown on the Mexican plateau some 7,000 years ago, and if teosinte is wild maize, which is almost certain, it must have been taken into cultivation considerably earlier than during the Coxcatlán culture phase of Tehuacán. Teosinte does not occur in the arid Tehuacán Valley, but is distributed along the western escarpment of the mountains and the wetter parts of the Mexican plateau (Wilkes, 1977).

From its center of domestication in Mesoamerica maize spread rapidly across the Americas. It is known to have been cultivated in New Mexico and Arizona not later than 4000 B.P. (Mangelsdorf, Dick & Cámara-Hernández, 1967), and also reached northwestern Mexico as a cereal some 4,000 years ago (Mangelsdorf, MacNeish & Galinat, 1967b). Maize was grown in Ecuador during the early formative stage dating back some 5,000 years (Zevallos et al., 1977).

In the Americas maize evolved with beans (*Phaseolus vulgaris* L. and *P. lunatus* L.), squash (*Cucurbita* spp.), and amaranths as staple foods (Kaplan, 1965; Gentry, 1969; Baudet, 1977). Only in the wet tropics and high Andes are tubers more important than maize. Indeed, maize is such an excellent cereal, with such good nutritious qualities and a wide range of adaptations, that its domestication probably excluded several other potential cereals from being taken into cultivation. It is known that maize replaced *Setaria geniculata* in Mexico and *Bromus mango* in Chile as planted cereals.

Indian wild rice (*Zizania aquatica*) is a newly domesticated cereal. The species is widely distributed in temperate North America from the Dakotas east to the Atlantic coast and south to Florida and Texas. In the northeast, and in Wisconsin, Minnesota, and adjacent Canada wild rice is extensively harvested. Hofstrand (1970) estimates that some 40,000 acres of natural stands are commercially harvested in Minnesota and Wisconsin alone.

The range of wild rice has probably been extended by sowing ever since it was first used as a cereal. It is easy to establish along shores of shallow lakes. Attempts to grow *Zizania* successfully, however, have until recently failed. The first serious attempts to grow wild rice commercially in paddies date back less than two decades (Oelke et al., 1973). Since 1971 production of wild rice in man-made habitats exceeds that harvested from natural stands in Minnesota (Brunson, 1972). Success in growing *Zizania* followed the discovery of a population with poor seed dispersal ability. It is estimated that in wild stands some 90% of grain escapes the harvester due to natural seed dispersal. Less than 50% of the grain is naturally dispersed in improved races grown commercially (deWet & Oelke, 1978).

Origins and Consequences of Food Production

The shift from hunting and food gathering to animal and plant husbandry ranks with the industrial revolution as one of the great achievements of man. Hunting-gathering is not necessarily a difficult way of life. Gathering wild food is less labor demanding than growing the same plants for food (Bronson, 1977). Bushmen and other present-day nomadic hunter-gatherers devote at most a few hours a day to subsistance activities (Lee, 1972). However, a nomadic way of life limits cultural evolution. Settled communities demand a regular food supply in the area of settlement. This is best achieved through agriculture.

Why the shift from hunter-gatherer to settled agriculturist occurred during the culture history of man is not known. Man must have had a basic knowledge of plant cultivation long before he actually started to domesticate plants by consciously sowing what was harvested from a planted population. The Indians of the Great Basin of western North America were specialized harvesters of wild cereals, who sowed to increase the population density of the fields to be harvested. Similarly, gardens of wild food plants are often maintained around temporary settlements of nomadic herdsmen. Sowing experiments are continued for a few generations and then abandoned.

Plant and animal husbandry evolved over several millennia, and settled farming is a relatively recent innovation of man that does not date back much beyond 10,000 years. The possible reasons why farming did not evolve earlier during the culture history of man are discussed by Bronson (1977). He suggests four possible explanations for this delay in food production. The first is labor saving. As already pointed out, gathering plant food and hunting are less labor intensive than farming. Second, time was required for reliable cultivated crops to evolve. Food crops probably were grown for millennia before evidence of domestication became obvious in the archaeological record. Third, farming de-

veloped as an adaptive response to increase in population numbers. Plant husbandry was not necessary when populations were small (Cohen, 1977). Fourth, farming involves risk. The hunter-gatherer had to invest a substantial amount of labor and resources in growing food crops without a guarantee of success. Crop failure is still common and often leads to famine.

Smith (1972) suggests that food production was initiated on a number of occasions by different groups of hunter-gatherers when faced with a gradual reduction in productivity of effort required to maintain the "culturally approved standard of living and the traditional group size and social organization." Once initiated, population pressures in particular will tend to demand and intensify agricultural activities.

A combination of these and other factors probably led to the beginnings of agriculture. From a botanical point of view, certain species lend themselves to domestication while others are almost impossible to domesticate (deWet & Harlan, 1975; deWet, 1979). American wild rice, *Zizania aquatica*, does not readily adapt to man-made habitats. Although it was extensively sown in natural habitats, it was not domesticated by Amerinds (Dore, 1969; deWet & Oelke, 1978). Only natural colonizers are readily cultivated as annual seed crops. Planting of seeds harvested from previously man-sown populations may have first become important to preserve selected traits. It seems likely that teosinte was taken into cultivation to preserve a newly discovered tunicate allele. The oldest known maize from Tehuacán is distinctly tunicate. It has soft, papery glumes. This mutation not only induces some stability to the rachis of teosinte, and thus facilitates harvesting, but also greatly enhances threshing the grain from the otherwise indurated glumes. The common characteristic of domesticated cereals, their inability of natural seed dispersal, may also have been a trait that was consciously selected by man. Harvesting by sickle (Wilke et al., 1972) in association with sowing (Harlan et al., 1973), however, automatically leads to a gradual loss of mechanisms for efficient natural seed dispersal. Be that as it may, wherever grasses were extensively harvested and agriculture was possible, selected species that were preadapted to withstand habitat disturbances by man eventually became domesticated.

Cereal agriculture seems to be oldest in Southwest Asia. Carter (1977) argues that the idea of plant and animal husbandry spread slowly from this nuclear center across the Old World and eventually to the Americas. Conclusive evidence for a diffusion of the knowledge of agriculture between the Old and New Worlds is lacking, however, and it seems more likely that agriculture evolved independently in several regions of the Old and New Worlds. Different species were domesticated at different times in the Near East, Far East, African savanna, and New World without evidence of exchange of crops among centers during the earlier stages of domestication. Civilizations developed independently in the Old and New Worlds until late historical times. Accidental contacts may have occurred between Europe and the east coast of North America, and between the west coast of both Mesoamerica and South America and Asia (Carter, 1977; Lathrap, 1977). However, even if true, cultural exchange must have been minimal. It was not until the fifteenth century that Old World crops were brought to the New

World in exchange for such important New World crops as maize, potato, sweet potato, garden beans, tomato, and peppers.

Cultural contact between the Near East and Europe is obvious in the archaeological record at least since 8000 B.P. Near Eastern agriculture also spread to ancient Egypt where wheat and barley became the basis on which dynastic Egypt was built. Near Eastern influences probably reached the African savanna civilizations around the seventh century A.D. with the expansion of Islam across North Africa (Lewicke, 1974). Sorghum races that evolved in India after some 3,000 years of isolation were reintroduced to Africa during this time (Harlan & Stemler, 1976). Contact of the Near East with the Far East occurred around 1500 B.C. when wheat and barley reached China (Ho, 1969).

Food production has advantages over food gathering. However, several societies never adopted agriculture. The aborigines of Australia, the bushmen of southern Africa and several jungle tribes in Africa, Asia and the Americas, even today shun a settled way of life. Comparing these hunter-gatherer societies with farmers, it is obvious that food production has substantially accelerated the social evolution of man during the 400 or so generations since the beginnings of cereal cultivation (Childe, 1936).

What are the consequences of food production? Rousseau (1755) argues that agriculture made organized work a necessity, forests were destroyed to make way for crops, individual ownership of property was introduced, and slavery developed. Survival of "civilized" man became dependent on cereal agriculture. Overpopulation, depletion of the world's resources, planetary pollution, and the social ills of cities are penalties we have to pay for the pleasure of an abundant and stable food supply.

The social consequences of village life are discussed by Smith (1972), and fall outside the scope of this manuscript. More important from the point of view of a botanist is the impact of farming on the immediate environment. Food production permits a greatly increased population density per unit area over that characteristic for hunter-gatherers. Cipolla (1964) estimates that the world's population was between five and ten million some 10,000 years ago when man first practiced conscious plant and animal husbandry. Hunter-gatherers live in equilibrium with the environment and have little lasting effects on nature. Farming by its very nature destroys the natural environment. Habitats are permanently altered, and a return to hunting and food gathering becomes impossible. Food production, for better or for worse, is here to stay. We must learn to cope with the pleasures as well as ills of civilization.

Weeds and domesticates evolved in the permanently disturbed man-made habitat. Domesticates are cared for, and we depend on them for our food supplies. They are carefully selected for total fitness in specific environments, and their population sizes are carefully controlled by man. Weeds are spontaneous in the man-disturbed habitat. Great effort is required to maintain their population growth, lest they totally colonize the habitat in which man grows his crops. Man, the ultimate weed, must learn to control his own population growth. Food production can keep pace with the human population explosion for the immediate future. However, planetary pollution, shortages of natural resources, and the

numerous social ills that accompany overpopulation are problems that will intensify. Only when these problems are solved can man hope to again live in harmony with his environment.

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THREE NEW SPECIES OF *FLOURENSIA* (ASTERACEAE-HELIANTHEAE) FROM SOUTH AMERICA[1]

Michael O. Dillon[2]

Abstract

Three new species of *Flourensia* (Asteraceae-Heliantheae) from South America are described: *F. peruviana* Dillon and *F. polycephala* Dillon from central and southern Peru respectively; and *F. blakeana* Dillon from northcentral Argentina.

The genus *Flourensia* is represented by at least four species in Peru, two of these described for the first time within this paper. *Flourensia macrophylla* Blake is represented by scattered populations in valleys of various rivers draining into the Pacific along the western slope or Cordillera Occidental from northern to central Peru (2,500–3,500 m). *Flourensia angustifolia* (DC.) Blake is found in intermontane valleys associated with the tributaries of the Río Perené and Río Huallaga in the Cordillera Central (1,700–3,300 m). *Flourensia peruviana* Dillon and *F. polycephala* Dillon are distributed in dry sites in valleys with eastern drainage from southcentral and southern Peru. *Flourensia heterolepis* Blake is represented by scattered populations in the Cordillera Real of southeastern Bolivia (ca. 2,700 m), a distance of ca. 725 km from the southeastern Peruvian taxa. Each species is readily distinguished by a complement of morphological characters and a distinct geographical distribution. The distributional pattern of these taxa corresponds with regions postulated to have undergone a series of humid-arid cycles during the Quaternary, which drastically and repeatedly altered vegetation patterns (Vuilleumier, 1971; Simpson, 1975). While it is difficult to accurately determine when and how these taxa attained their present distributions, a rather recent radiation is suggested. A similar pattern of species distribution is exhibited in other taxa occupying various habitats in the Peruvian Andes (Simpson, 1975). An additional example is found in *Tecoma* (Bignoniaceae) (Gentry, 1979) which has unique taxa in each of the major valleys similarly occupied by different *Flourensia* species.

The following key compares the salient differences between all the *Flourensia* species of Peru and adjacent Bolivia. Figure 1 illustrates the distribution of these species.

1a. Leaves shallowly denticulate.
  2a. Leaves oval to oblong-oval, the apex obtuse to subobtuse .... *F. macrophylla*
  2b. Leaves lanceolate to narrowly-elliptic, the apex acute .... *F. angustifolia*
1b. Leaves strictly entire.
  3a. Outer phyllaries 2–3 mm long, the inner 3–5 mm long, all ca. 1.5 mm wide .... *F. peruviana*

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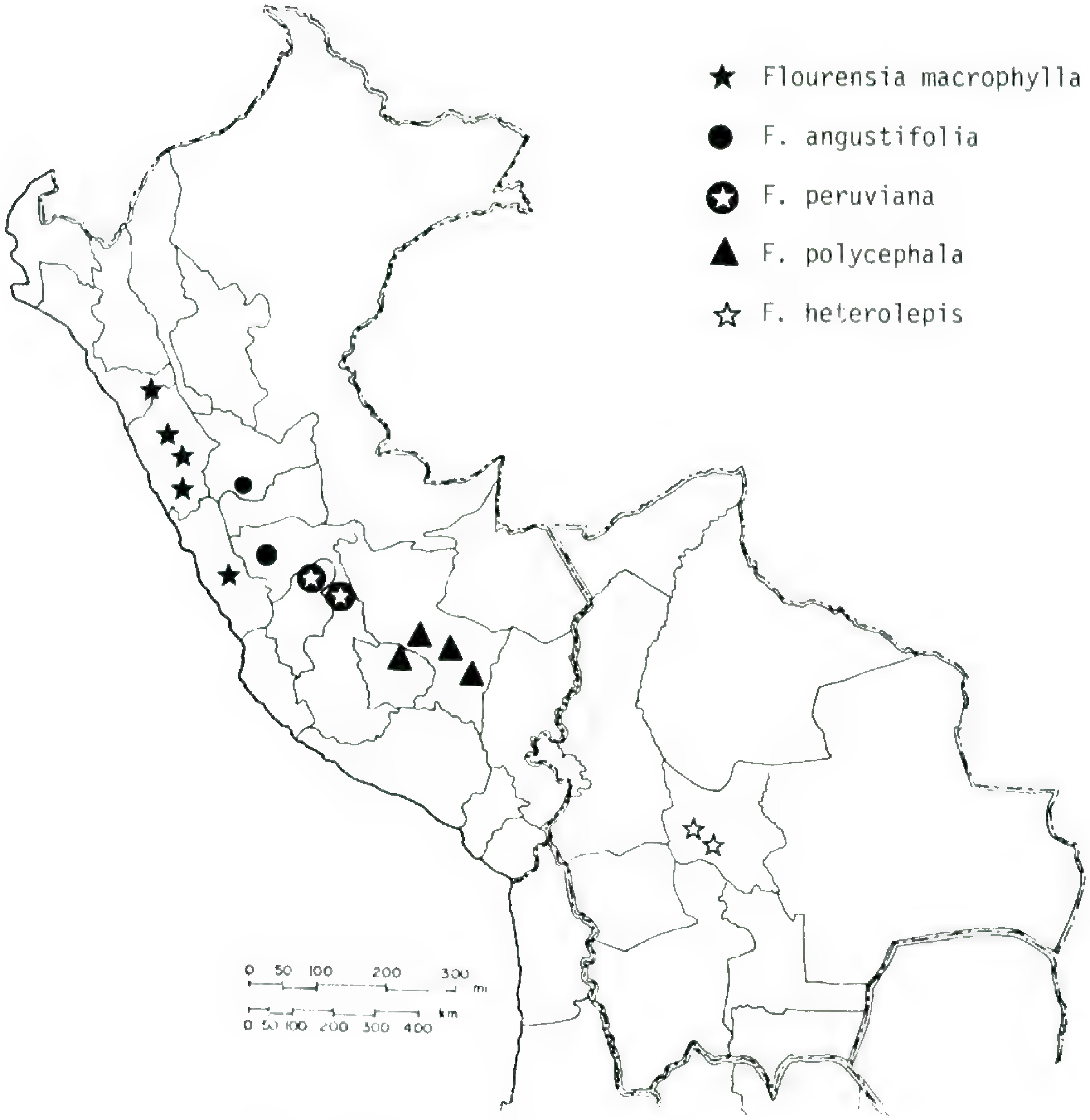

FIGURE 1. Distribution map of *Flourensia* species in Peru and adjacent Bolivia.

3b. Outer phyllaries 5–9 mm long, the inner 8–10 mm long, all (1–)2–3(–3.5) mm wide.
 4a. Inflorescences 2–5-flowered, terminal and axillary (central Bolivia) ...... *F. heterolepis*
 4b. Inflorescences 4–8-flowered, cymose ...... *F. polycephala*

Flourensia polycephala Dillon, sp. nov.—Fig. 2.

Species haec ab *F. heterolepis* Blake differt capitulis numerosis, inflorescentia cymosa, phyllariis extimis (5–)7–8 mm longis, ca. 1 mm latis, intimis rhombeo-ovatis, 8–9 mm longis, 3.0–3.5 mm latis, floribus radii 10–13, pappo saepe articulato.

Shrub to 4 m; branchlets striate, resinous. *Leaves* lanceolate, to lance-elliptic, (8–)10–12(–14) cm long, 1.5–2.5(–3.0) cm wide, entire, acute or rarely obtuse, broadly acuminate, the margins strigillose; petioles 2–5 mm long. *Inflorescence* 4–8-flowered, cymose-paniculate; peduncles (1–)3–5(–7) cm long. *Capitula* 1.0–1.5 cm wide (excluding the ray florets), 1.5–2.0 cm high; involucre graduated, 3-seriate; outer phyllaries linear-lanceolate, (5–)7–9 mm long, ca. 1 mm wide,

FIGURE 2. *Flourensia polycephala* Dillon, ×¾. [After *Marin 231* (F).]

acute, glandular, keeled, the inner phyllaries rhombic, 8–9 mm long, 3.0–3.5 mm wide, attenuate, laterally chartaceous, glandular, keeled; paleas ca. 9 mm long, ca. 3 mm wide, acute to obtuse, erose, glandular; ray florets 10–13, the ligules oblong, ca. 3 cm long, 5–6 mm wide, the tube ca. 5 mm long; disc florets 20–30, ca. 7 mm long, cylindric-campanulate. *Achenes* obconical, 8–9 mm long, ca. 3 mm wide, depressed ovate in cross-section, villous; pappus of 2 awns, ca. 3 mm long, readily disarticulating, squamellae absent.

TYPE: PERU. CUZCO. Pisac, Apr. 1943, 3000 m, *Marin 231* (LIL, holotype; F, isotype).

Flourensia polycephala differs from *F. heterolepis* Blake in having more nu-

merous capitula and cymose inflorescences. It differs from its nearest geographic neighbor, *F. peruviana*, in having longer phyllaries and more ray florets.

This species is known from dry, rocky slopes in the quebradas associated with the Río Apurimac and Río Urubamba in southeastern Peru (2,700– 3,200 m) (Fig. 1). Flowering Jan.–Apr.

Additional Specimens Examined: PERU. APURIMAC: Grau, Orepeza Valley, *Vargas 9784* (F, UC). CUZCO: *Ellenberg 1000* (US). Huasao, *Herrera 3098* (US). Urubamba, lower end of Quebrada Pumahuanco, ca. 2–4 km NW of Urubamba, *Iltis et al. 854* (US). Urubamba, *Lamallva 53* (LPS); Hda. Urco, Vilconota Valley, *Vargas 638* (MO). Rumichaca, *Vargas 9597* (LIL). Chicón Canyon, *Vargas 11053* (UC).

Flourensia peruviana Dillon, sp. nov.—Fig. 3.

Species haec ab *F. polycephala* Dillon differt involucro minore, phyllariis reductis aliter isdem, foliis magnitudine formaque similiter *F. angustifolia* (DC.) Blake, cognata approximatissiam, sed differt folia integra. Pappus acheniorum interdum artisis disarticulatis duo 3 mm longis confectus.

Shrub to 2 m; branchlets striate, resinous. *Leaves* lanceolate to oblong-lanceolate, (5–)7–10(–12) cm long, (1.0–)1.5–2.0 (–3.0) cm wide, entire, acute to obtuse, broadly acuminate, the margins strigillose; petioles (2–)4–8(–10) mm long. *Inflorescence* 4–8-flowered, cymose-paniculate; peduncles 0.5–5.0 cm long. *Capitula* 7–10 mm wide (excluding ray florets), ca. 10 mm high; involucre graduated, 2–3-seriate; outer phyllaries lanceolate, ca. 2 mm long, ca. 1 mm wide, acute, glandular, keeled, the inner phyllaries elliptic-obovate, ca. 5 mm long, ca. 1.5 mm wide, laterally chartaceous, glandular, keeled, acute; paleas ca. 9 mm long, rounded apically, erose, glandular; ray florets 8–10, the ligules oblong to oval, 10–18 mm long, ca. 5 mm wide, the tube ca. 5 mm long; disc florets 20–40, ca. 7 mm long, cylindric-campanulate. *Achenes* obconical, ca. 10 mm long, 2–3 mm wide, depressed ovate in cross-section, villous; pappus of 2 slender awns, ca. 3 mm long, readily disarticulating, squamellae absent.

TYPE: PERU. HUANCAVELICA: Checcyancu a 4 km E of Conaica, 3000–3500 m, 14 Mar. 1971, *Tovar 193* (US, holotype; LPS, USM, F, isotypes).

Flourensia peruviana differs from *F. polycephala* in possessing a much smaller involucre with the phyllaries reduced in size, but essentially the same shape. Its leaves are comparable in size and shape to *F. angustifolia* (DC.) Blake, its nearest geographic neighbor, but differ in having strictly entire margins. This species is known from southcentral Peru on dry, rocky slopes in the quebradas associated with the Río Mantaro (1,700–3,500 m) (Fig. 1). Flowering Mar.–Apr.

Additional specimens examined: PERU. AYACUCHO: La Mejorada to Ayacucho, KM 15, *Ochoa 574* (GH). Huamanga, Chaquihuaycco, arriba de Ayacucho, *Tovar 5491* (USM). Chanchara, Río Cachi, *Tovar 5589* (USM). Alrededores de Ayacucho, *Tovar 5709* (USM). HUANCAVELICA: Tayachaja, between Izuchaca and Mariscal, *Tovar 1378* (LPS).

Another new species of *Flourensia* from Argentina may also conveniently be described here.

Flourensia blakeana Dillon, sp. nov.—FIG. 4.

Frutex 0.4–1.0 m alto, ramoso, cortice cana ad nigra, ramulis nigris. Folia (1.5–)2.0–3.5(–4.7) cm longa, (0.3–)0.4–0.8(–1.1) cm lata, anguste oblongo-elliptica, acuta, acuminata, integra, marginibus strigillosis; petiolis 1–3 mm longis. Capitula 1–4, terminales axillaresque, cymosa (5–)7–10(–14) mm

FIGURE 3. *Flourensia peruviana* Dillon, ×¾. [After *Tovar 193* (F).]

FIGURE 4. *Flourensia blakeana* Dillon, ×⅔. [After *Dillon & Rodríguez 560* (F).]

lata, 6–11 mm alta, pedunculis 1–4 cm longis, involucro 2-seriato, phyllariis aequalibus (3–)4–6(–7) mm longis, ca. 1 mm latis, extimis lineario-lanceolatis, intimis anguste rhombeis, attenuatis, herbaceis, nigris, basim strigillosis, paleis 5–6 mm longis, obtusis, nigellis. Flores radii ca. 8, disci ca. 25, corollis ca. 4.5 mm longis, cylindricis-campanulatis. Achenia obconica, ca. 6 mm longa, ca. 2 mm lata, villosa, pappi aristis duo ca. 3.5 mm longis persistentibus confecti, squamellis carentes. Chromosomatum numerus $n = 18$.

Much-branched *shrub,* 0.4–1.0 m tall, the bark gray to black; branchlets black. *Leaves* narrowly oblong-elliptic, (1.5–)2.0–3.5(–4.7) cm long, (0.3–)0.4–0.8(–1.1) cm wide, acute to acuminate, entire, the margins strigillose; petioles 1–3 mm long. *Inflorescence* cymose, 1–4-flowered; peduncles 1–4 cm long. *Capitula* (5–)7–

10(–14) mm wide (excluding the ray florets), 6–11 mm high; involucre 2-seriate; phyllaries (3–)4–6(–7) mm long, ca. 1 mm wide, black, the outer linear-lanceolate, the inner narrowly rhombic, attenuate, herbaceous, the bases strigillose; paleas 5–6 mm long, obtuse, blackish; ray florets ca. 8, the ligules oblong-oval, 1.0–2.4 cm long, 5–8 mm wide, the tube 3–4 mm long; disc florets ca. 25, the corollas ca. 4.5 mm long, cylindrical-campanulate. *Achenes* obconical, ca. 6 mm long, ca. 2 mm wide, villous; pappus of 2 awns, ca. 3.5 mm long, persistent, squamellae absent. Chromosome number: $n = 18$.

TYPE: ARGENTINA. TUCUMÁN: Km 95–105 on Rt. 307, between Amaichá del Valle and Tafí del Valle, 2900–3000 m, 22 Feb. 1973, *Dillon & Rodríguez 560* (TEX-LL, holotype; F, MO, isotypes).

Flourensia blakeana is a frequent element of the xeric shrub formation in the Cuesta del Infiernillo, usually associated with *Psila boliviensis* and various *Senecio* species. It most closely resembles *F. fiebrigii* Blake, from the mountain valleys of southwestern Bolivia and adjacent Argentina, but the latter is distinguished by its larger leaves and more robust habit, and by a generally more pubescent involucre. The specific epithet commemorates Sidney F. Blake (1892–1959), noted American synantherologist.

Additional specimens examined: ARGENTINA. CATAMARCA: Santa María, Torollaco, *Reales 1056* (LIL). Pafanquillo, *Reales 1702* (LIL). TUCUMÁN: Ca. 25 km NW of Tafí del Valle, *Bacon & Bohnstedt 77* (TEX-LL). Cuesta del Infiernillo, *Cabrera & Frangi 20763* (LPS). Devisadero, Cafayate–Tafí del Valle, *Carenzo 1358* (LIL). Cardones, *Castillon 3274* (A). Alto del Fio, *Castillon 3115* (LIL). Tafí, KM 95, Los Cardones, camino del Infiernillo a Amaichá, *Legname & Vervoorst 34* (NY). Machorastroja, *Schreiter 1311* (LIL). Amaichá to Santa María, *Schreiter 5636* (A, LIL). Las Arcas, *Schreiter 5637* (A, LIL). Quebrada del Chorro, *Venturi 4110* (LIL, US).

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NEW SPECIES AND A NEW COMBINATION IN PALMAE, THEACEAE, ARALIACEAE, APOCYNACEAE, AND BIGNONIACEAE FROM THE CHOCO AND AMAZONIAN PERU[1]

Alwyn H. Gentry[2]

Abstract

Several new species from the Chocó region of western Colombia and adjacent Ecuador and from Amazonian Peru are described—*Aiphanes chocoensis* A. Gentry (Palmae), *Freziera dudleyi* A. Gentry, *F. jaramilloi* A. Gentry and *F. sessiliflora* A. Gentry (Theaceae), *Schefflera megacarpa* A. Gentry (Araliaceae), *Bonafousia chocoensis* A. Gentry and *Mandevilla dodsonii* A. Gentry (Apocynaceae), *Memora juliae* A. Gentry and *M. pseudopatula* A. Gentry (Bignoniaceae). The new combination *Rauvolfia aphlebia* (Standl.) A. Gentry is proposed for the plant previously known as *Rauvolfia sarapiquensis* Woods. and the species is reported for the first time from South America.

The Chocó region of western Colombia and adjacent Ecuador and Peruvian upper Amazonia are potentially two of the richest areas of the world floristically (Gentry, 1978, 1979, 1981). Both remain very poorly known botanically and current collecting programs in these regions are turning up many undescribed species. It is the purpose of this paper to describe several of the striking new species discovered in the course of these collecting programs in groups for which no taxonomic specialist is available.

PALMAE

Aiphanes chocoensis A. Gentry, sp. nov.

Palma parva, acaulis. Folia indivisa marginibus erosis, costis dense spinosis, spinis mollibus brevibusque, supra nervibus secundariis spiniferis. Spadix simplex, spicatus, pedunculo ca. 60 cm longo, parce spinoso. Flores 2 mm longi, sepalibus membranaceis, petalis masculinis ovatis, staminibus 6, antheris minutis, petalis femineis late ovatis. Fructus non visus.

Stemless palmlet. Leaves completely undivided except the bifid apex, ca. 65 cm long, ca. 25 cm wide at the widest point, the margin prominently erose, with ca. 17 equally spaced primary lateral nerves, the midrib and petiole densely spiny with short soft brownish spines mostly ca. 0.5 cm long (rarely to 1 cm long), the lamina below minutely puberulous and without spines (a single 6 mm long spine on one secondary nerve in the MO isotype), above glabrous and with lines of 0.8–1.8 cm long spines spaced rather evenly ca. 1 cm apart along the main lateral nerves, numerous noticeable dark transverse striations perpendicular to the main lateral veins above. Spathe (only fragments seen) spiny with short few-millimeter long brownish spines. Spadix spicate, completely unbranched, the peduncle ca.

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60 cm long, rather sparsely spiny-hirsute with soft few-millimeter long spines; fertile part of spike 18 cm long, the rachis between the flowers hirsute from the small soft brownish spines. Flowers white, 2 mm long, the sepals thin and membranous, the petals of the male flowers ovate, coriaceous, obtuse to acutish, straw colored when dry, the stamens 6, the anthers very short and thick, as long as wide, ca. 0.3 mm long, the filaments ca. 0.3 mm long; petals of female flowers broadly ovate, obtusely triangular, greenish-tipped when dry, the staminodial cup dentate, ca. 1 mm long. Fruit not seen.

Type: Colombia. chocó: Río Mutatá, tributary of Río El Valle between the base of Alto del Buey and mouth of river, tropical wet forest, 100–150 m, 9 Aug. 1976, *Gentry & Fallen 17450* (COL, holotype; MO, BH(sterile), isotypes).

Fairly common locally along the Río Mutatá but to date not seen elsewhere in the Chocó.

Only two species of *Aiphanes* with unbranched spicate inflorescences were known by Burret (1932, 1937, 1940). Several additional species of *Aiphanes* have subsequently been described (Dugand, 1944; Bailey & Moore, 1949; Moore, 1951), but none of these has unbranched inflorescences or undivided leaves. Both of the known species with spicate inflorescences—*A. monostachys* Burret and *A. simplex* Burret—are Colombian but have pinnately compound leaves and occur at higher altitudes. No other species of *Aiphanes*, except *A. eggersii* Burret and *A. caryotifolia* (H.B.K.) Wendl., both with divided leaves and branched inflorescences, occur in the trans-Andean lowlands. Despite its undivided leaves, the new species can be referred with certainty to *Aiphanes* rather than *Bactris* because of its erose leaf margin.

While Burret's synopsis of *Aiphanes* leaves much to be desired, there is no doubt as to the novelty of *A. chocoensis*, the only species of *Aiphanes* combining an unbranched inflorescence and undivided leaf. Thus the probability that most of the 31 species of *Aiphanes* recognized by Burret and subsequent authors will prove synonymous is irrelevant to the validity of *A. chocoensis*.

I thank Harold Moore for confirming, from the sterile duplicate available to him, that this plant belongs to *Aiphanes* and for giving me the encouragement necessary to delve into a group as taxonomically difficult as the palms.

THEACEAE

Freziera dudleyi A. Gentry, sp. nov.

Arbor grandis, ramulis tomentosis permanentibus. Folia lineari-oblonga, acuminata, obtuse cuneata, sessiles, serrulata, glabrata. Flores axillares, fasciculati, pedicellis 1–2 mm longis, calycibus glabris, ovario ovoideo, tres stigmatis. Fructus ovoideus, 5 mm longus.

Canopy tree 30 m or more tall; branchlets persistently appressed- to subappressed-tomentose, with small round lenticels when older. Leaves linear-oblong, acuminate, obtusely cuneate and slightly inaequilateral at the base, serrulate, the serrulations gland tipped, the gland sometimes terminating in a caducous tooth, 5–12 cm long, 1.2–2.2 cm wide, completely glabrous above, glabrescent below, usually with a few persisting long appressed trichomes along the midvein, the midvein prominent above and below, the secondary veins not evident, conspic-

uously longitudinally lined parallel to the midvein, practically sessile, the pedicel ca. 1 mm long. Flowers axillary and ramiflorous, fasciculate, 2–4 per fascicle, pedicels short, 1–2 mm long, glabrous; bracteoles suborbicular, with a glandular tip, ca. 2 mm long, minutely puberulous only near the apex; calyx lobes orbicular, 2–3 mm in diameter, glabrous except the slightly ciliate margins of the outer sepals; ovary ovoid, 2 mm long, tapering into a short thick style ca. 0.5 mm long, the stigmas 3. Immature fruit ovoid, 5 mm long.

TYPE: PERU. CUZCO: Cordillera Vilcabamba, Province La Convención, 73°30′W, 12°30′S, common in dense cloud forest at camp 2-1/2 1730 m, ca. 14 km walking distance NE from Hacienda Luisiana and the Apurimac River, immense A-story tree 100 or more feet tall, d.b.h. 24 in., crown flat and spreading, ca. 60 ft. wide, 30 ft. tall, laden with epiphytes, leaves willow-like, mature leaves glossy dark green above, pale and glossy below, 1st year leaves silvery canescent below, bronzy when young, flowers cauliflorous with dark purple stigmas, bark of branchlets conspicuously white speckled on dark brown, extending from 1500 m to 2000 m alt., 28 June 1968, *T. R. Dudley 10567* (MO, holotype).

This outstanding new species has the narrowest leaves in the genus. In Kobuski's (1941) monograph it keys to *F. nervosa* H.&B. or *F. karsteniana* (Szyszyl.) Kobuski depending on whether its leaf base is considered obtuse or cuneate. Both these Colombian species have much wider leaves with noticeable secondary veins.

Freziera jaramilloi A. Gentry, sp. nov.

Frutex, ramulis tomentosis permanentibus. Folia anguste elliptica, acuta vel subacuminata, cuneata, subtiliter serrata, infra tomentosa, petiolo 2–5 mm longo. Flores axillares, fasciculati, pedicellis 1–2 mm longis, calycibus glabris praeter margines, ovario globoso. Fructus globosus, ca. 5 mm diametro.

Shrub 2.5 m; branchlets persistently subappressed grayish tomentose, elenticellate. Leaves narrowly elliptic, acute to subacuminate, cuneate and aequilateral at the base, sharply finely serrate, 3.5–6 cm long, 1.3–2 cm wide, glabrous above except the appressed pubescent midvein, the 11–13 pairs of secondary veins plane, separated by 2–4 mm, below conspicuously and uniformly appressed tomentose with grayish trichomes; petiole 2–5 mm long, appressed tomentose. Flowers axillary, 1–2 per fascicle, short pedicellate, the pedicel puberulous and 1–2 mm long; bracteoles ovate, 1.5–2 mm long, glabrous except the ciliate margin; calyx lobes suborbicular, ca. 2 mm long and wide, glabrous except the ciliate margins; petals (in bud) ca. 5 mm long; ovary globose, the style slender, 2 mm long. Fruit red, globose, ca. 5 mm in diameter.

TYPE: COLOMBIA. CHOCÓ: Carretera Ansermanuevo–San José del Palmar, entre el Alto de Galápago y San José del Palmar, 1700–1940 m, 27 Aug. 1976, *E. Forero, R. Jaramillo, M. Pabón, J. Espina & Z. Piñeros 2201* (COL, holotype; MO, isotype).

This is one of the smallest-leaved species of *Freziera*, being matched only by *F. euryoides* Kobuski and *F. parva* Kobuski, and it keys out with this group in Kobuski's monograph. Both of these species have longer pedicels and reduced

leaf pubescence and serrulate leaves. In addition *F. jaramilloi* differs from *F. euryoides* in the secondary veins more numerous and closer together and from *F. parva* in fewer pairs of secondary veins; both those species are much less pubescent, especially lacking the conspicuously persistent branchlet tomentum of *F. jaramilloi*. Two other species of *Freziera* have even smaller leaves, about half as long as those of *F. jaramilloi*. *Freziera microphylla*, described subsequent to Kobuski's monograph, also differs from *F. jaramilloi* in such features as longer pedicels and puberulous sepals, and *F. suberosa* differs also in larger flowers and fissured corky bark.

Freziera sessiliflora A. Gentry, sp. nov.

Arbor, ramulis glabratis. Folia anguste elliptica, acuminata, cuneata, integra vel subintegra, infra sparce puberula trichomatibus longis subappressis, petiolo 2–3 mm longo. Flores axillares fasciculati sessiles, calycis lobis exterioribus glabris, lobis interioribus puberulis.

Tree; young branchlets whitish sericeous-pubescent with subappressed trichomes, soon glabrate, elenticellate. Leaves narrowly elliptic, acuminate, cuneate and almost aequilateral at the base, almost completely entire to barely subserrulate, 7–8 cm long, 2.3–3 cm wide, glabrous above, the midrib raised, the secondary veins plane and hardly evident, below minutely lepidote and pubescent with scattered long whitish subappressed trichomes, the secondary veins not evident; petiole 2–3 mm long, merging with the leaf base. Flowers axillary, ca. 1–3 per fascicle, completely sessile; bracteoles glabrous, suborbicular, ca. 2 mm long and broad; calyx lobes orbicular, 2–3 mm long and broad, the outer lobes glabrous, the inner lobes puberulous except in the central third.

TYPE: COLOMBIA. CHOCÓ: Carretera Ansermanuevo–San José del Palmar, entre el Alto de Galápago y San José del Palmar, 1900 m, 29 Aug. 1976, *E. Forero, R. Jaramillo, M. Pabón, J. Espina & Z. Piñeros 2320* (COL, holotype; MO, isotype).

In Kobuski's key this species keys out to *F. sericea* if the glabrous outer calyx lobes are used and to *F. tomentosa* if the puberulous inner ones are used. Both of those species differ strikingly in having much larger (over 15 cm long), very much more pubescent leaves.

ARALIACEAE

Schefflera megacarpa A. Gentry, sp. nov.

Arbor parva. Folia palmatim composita, ca. 25 foliolata, foliola in 3 verticilli concentrici, sparsim minute puberula trichomatibus malpighiaceis. Inflorescentia ampla, aperta, terminalis, ramis no racemiformibus. Fructus subglobosus, 5-sulcatus, 15–18 mm longus, 12–15 mm latus.

Small tree 4–10 m; branchlets ca. 2 cm thick, the bark longitudinally striate. Leaves palmately compound, ca. 25-foliolate (few-foliolate on reduced leaves at the base of the panicle), the leaflets in 3 concentric whorls; leaflets of outermost whorl largest, to 16 cm long and 7 cm wide, elliptic, long acuminate (acumen to 2.5 cm long), rounded to cuneate at the base, petiolules to 15 cm long; leaflets of the innermost whorl narrower and as small as 7 cm long and 1 cm wide; all leaflets

glabrous except for minute reddish appressed T-shaped trichomes along the main veins and widely scattered over the surface; petiole and petiolules minutely appressed-puberulous with reddish T-shaped trichomes. Inflorescence a large open terminal panicle ca. 60 cm long, the branches not racemiform, sericeous rufescent with T-shaped trichomes, the peduncles of the ca. 5-flowered ultimate umbels 1.5–3 cm long, the pedicels (in fruit) 1.5 cm long. Flowers not seen. Fruits basically subglobose, longitudinally deeply 5-sulcate, puberulous with appressed T-shaped trichomes, 15–18 mm long, 12–15 mm wide, the stigma persistent at the apex, each of the 5 stigma branches almost 2 mm long.

TYPE: PERU. LORETO: Province Requena, Genaro Herrera, Río Ucayali, non-inundated forest on mixed sand and clay soil, 7 Dec. 1977, *Gentry, Revilla, Ruiz & Vasquez 21225* (MO, holotype; AMAZ, F, INPA, NY, USM, isotypes).

This remarkable species apparently has the largest fruits of any New World Araliaceae and the most leaflets. It may have the most leaflets per leaf of any palmately compound-leaved plant in the world. It belongs to the group of *Schefflera* species with open paniculate inflorescences with nonracemiform lateral branches which includes *S. gracillima* Steyerm. & Maguire, *S. japurensis* (Mart. & Zucc.) Harms, *S. macrocarpa* (Cham. & Schlecht.) Frodin (ined.), *S. pachycarpa* (March.) Frodin (ined.) *S. paraensis* Hub., *S. umbellata* (N.E. Br.) Vig. Most of the species in this group differ in strongly whitish pubescent leaf undersides and all have much smaller fruits. Vegetatively, *S. megacarpa* is similar to *S. confusum* (March.) Harms, and a sterile collection from Amazonian Brazil, *Krukoff 8808* (F), determined as *Schefflera* cf. *confusa* by Frodin, is probably referable to *S. megacarpa*.

APOCYNACEAE

Bonafousia chocoensis A. Gentry, sp. nov.

Frutex. Folia elliptica vel obovato-elliptica, acuminata, subcordata, sessilia, plus minusve amplexicaulia. Inflorescentia flore solitario axillari. Calyx lobis ovatis, 2 mm longis; corolla lutea pallida, lobis angustis, spathulatis. Fructus non visus.

Shrub 1 m tall; branchlets somewhat angulate, lactiferous. Leaves elliptic to obovate-elliptic, acuminate, rounded to subcordate at the base, 7–19 cm long, 3.5–9.5 cm wide, completely sessile, more or less amplexicaul. Inflorescence a single flower, the pedicel glabrous, ca. 2 mm long; calyx lobes membranous, ovate, 2 mm long; corolla salverform, light yellow or cream, the tube 1.5 cm long and 2 mm wide, twisted and slightly narrower at the top, the reflexed lobes narrow, spatulate, ca. 8 mm long; stamens attached ca. 8 mm from the base of the corolla tube, the anthers subsessile, over 4 mm long. Fruit subglobose, 2.5–3 cm long, 2–2.5 cm wide; seeds oblong, 7–8 mm long, longitudinally ridged.

TYPE: COLOMBIA. CHOCÓ: Upper Río Truandó, La Teresita, 100–200 m, shrub 1 m, flowers light yellow, 19 Jan. 1974, *Gentry 9406*, (COL, holotype; MO, Z, isotypes).

Additional Collections Examined: COLOMBIA. CHOCÓ: Río Truandó at junction with Quebrada Buche, *Raphia* swamp, 1 Apr. 1968, *Duke 15743* (MO). Trail from Camp Teresita to Río Salada, 14 June 1967, *Duke 12220* (MO).

This species is unique in the genus in its strikingly sessile leaves, this trait accentuated by the usually more or less cordate leaf base. It is none of the species listed by Markgraf (1939) in his review of *Tabernaemontana* and its segregates and Professor Markgraf has kindly examined a fragmentary duplicate and confirms that it represents a new species.

Rauvolfia aphlebia (Standl.) A. Gentry, comb. nov.

Tabernaemontana aphlebia Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 946. 1938. TYPE: Costa Rica, *Brenes 20551* (F).
Rauvolfia sarapiquensis Woods., Ann. Missouri Bot. Gard. 28: 271. 1941. TYPE: Costa Rica, *Skutch 3556* (MO, holotype).

The type of *Tabernaemontana aphlebia* at the Field Museum is obviously conspecific with *Rauvolfia sarapiquensis*. Perhaps the detached leaves of the rather unsatisfactory type misled Standley to describe it under *Tabernaemontana*, although the leaf scars at the nodes show the typical whorled arrangement of *Rauvolfia*. Presumably its description in the wrong genus prevented Rao (1956) from checking *T. aphlebia* during his revision of *Rauvolfia* and caused Woodson to overlook the older name when describing *R. sarapiquensis*.

The species has an interesting disjunct distribution in the mountains of Costa Rica and Chiriquí Province of Panama (Gentry, 1974) and in the upper part of the Serranía de Darién on the border of Panama and Colombia where it has not been reported previously. On Cerro Tacarcuna it is a common and characteristic species of the montane oak forests above 1,400 m. Collections from the Darién/ Chocó border region include:

PANAMA. DARIÉN: Vicinity of Cerro Tacarcuna summit camp, 1500–1750 m, lower montane wet forest life zone, *Gentry & Mori 14040* (MO). West ridge of Cerro Malí half hour west of helipad, 1400 m, premontane wet forest, *Gentry & Mori 13830* (MO). South slope of westernmost peak of Cerro Tacarcuna massif, lower montane wet forest, 1500–1600 m, *Gentry, L. Forero, & H. Léon 16949* (COL, MO). COLOMBIA. CHOCÓ: Cerro Malí, 1420 m, *Gentry & Mori 13721* (MO).

Mandevilla dodsonii A. Gentry, sp. nov.

Frutex volubilis, caule hirsuto. Folia elliptica, acuminata, basi anguste cordata, infra dense puberula. Inflorescentia racemosa, axillaris, bracteis foliaceis, caducis. Calycis lobi setacei; corolla tubulo-campanulata, supra basin anguste tubularem; nectarium annulare.

Vine; stem terete, hirsute with trichomes 1–2 mm long. Leaves opposite, elliptic, the apex acuminate with a 1–2 cm long acumen, the base narrowly cordate, 9–17 cm long, 4–7.5 cm wide, membranous, above sparsely strigillose-puberulent, below rather densely puberulous with crisped whitish trichomes, strongly discolorous, glandular along the midrib above, the petiole 1.5-4 cm long. Inflorescence an axillary raceme, densely puberulous with subappressed trichomes, the pedicels ca. 5 mm long, the caudate-acuminate foliaceous bracts to 15 mm long and 5 mm wide, early caducous. Flowers with the calyx lobes setaceous, 13–15 mm long, sparsely puberulous; corolla tubular-campanulate above a narrowly tubular base, the upper tube (throat) somewhat gibbous, 3.5–5 cm long, 0.9–1 cm wide at the mouth, the narrow basal part of the tube 2–2.5 cm long, 6 mm wide at the extreme base and narrowed to 2 mm near the apex; anthers ca. 3.5 mm long, basally auriculate; ovary ovoid, 2-parted with a longi-

tudinal constriction, glabrous, ca. 1 mm long, its base surrounded by an apparently annular nectary ca. 1 mm long and 1.5 mm wide. Very immature fruit densely whitish villous.

TYPE: ECUADOR. LOS RÍOS/PICHINCHA (boundary disputed): Ridgeline at El Centinela, crest of Montañas de Ila on road from Patricia Pilar (km 45 on Santo Domingo-Quevedo road) to 24 de Mayo at km 12, 600 m, vine, flowers light yellow, 6 Feb. 1979, *C. Dodson, A. Gentry & J. Duke 7523* (MO, holotype; SEL, isotype).

Additional Collections Examined: ECUADOR. LOS RÍOS/PICHINCHA (boundary disputed): Same locality as type, 27 Nov. 1978, *Dodson 7294* (MO, SEL). ESMERALDAS: Ventanas, Km 319, Quito-San Lorenzo railroad, ca. 100 m, 7 July 1964, *Jativa & Epling 663* (MO).

This new species is very distinct from any known species of *Mandevilla*. The glandular midrib and gibbous corolla place it in subgenus *Exothostemon* where the large tubular-campanulate corolla and relatively large bracts relate it to *M. hirsuta* (A. Rich.) K. Schum. and its allies, according to Woodson's (1933) monograph. Vegetatively it is rather like *M. hirsuta* except for the somewhat different, more strongly discolorous indumentum, and one rather fragmentary specimen of this species at MO was identified as *M. hirsuta*. However, the totally different corolla shape (tubular-campanulate rather than tubular-infundibuliform) and long setaceous calyx lobes are very unlike *M. hirsuta*. The complete fusion of the nectaries into an annular ring would seem to be unique in *Mandevilla*.

Mandevilla dodsonii apparently is restricted to the strip of wet tropical forests along the western base of the Andes in northwestern Ecuador, a distribution presumably correlated with the Pleistocene forest refugium sometimes referred to as the Chimborazo refugium (Brown, 1975; Gentry, 1981).

BIGNONIACEAE

Memora juliae A. Gentry, sp. nov.

Frutex scandens, ramulis teretibus, lenticellis. Folia bipinnata, interdum cirrhis simplicibus; foliola elliptica vel anguste ovata, acuta vel acuminata, infra molliter villosa. Calyx spathaceus, membranaceus, glaber; corolla tubulo-infundibuliformis, glabra; ovarium lineare, sparce lepidotum; discus patelliformis. Capsula linearis complanatus, glabra, seminibus tenuibus, rectangularibus, quasi sine alis.

Liana; branchlets terete, slightly and glabrescently puberulous, drying brownish with conspicuous raised whitish lenticels, the nodes without interpetiolar glandular fields; pseudostipules minute, subulate to subfoliaceous, less than 7 mm long. Leaves typically bipinnately compound with 5–7 leaflets per pinna, the lower leaflets of each pinna often subdivided and 2–5-foliolate, the leaf thus 6–31-foliolate, sometimes with a simple tendril; leaflets elliptic to narrowly ovate, acute to acuminate, rounded to cuneate at the base, membranous to chartaceous, 2–11 cm long, 0.8–5 cm wide, softly villous below with erect rather scattered trichomes, above puberulous only along the main veins; petiole and petiolules puberulous. Inflorescence an axillary raceme, elongate or reduced, ebracteate, glabrous, the pedicels 0.7–1.7 cm long, glabrous or with a few subappressed trichomes, with a few large dark plate-shaped glands, with a pair of conspicuous

broad membranous foliaceous bracteoles 1–1.5 cm by 0.7–1 cm attached at the base of each calyx. Flowers with the calyx spathaceous, membranous, completely glabrous or slightly puberulous at the extreme apex, 20–30 mm long, 7–10 mm wide, drying olive brown or olive tan; corolla yellow, tubular-infundibuliform, (6–)7–9 cm long, 1.5–2 cm wide at the mouth of the tube, the tube 5–7 cm long, the lobes 1.5–2 cm long, completely glabrous except for a few minute glandular lepidote scales or lobes and stalked lepidote trichomes around the margins, villous below stamen insertion; stamens didynamous, the thecae divaricate, ca. 3 mm long, the filaments 2.5–3.5 cm long; pistil ca. 5 cm long, the ovary linear, 5–7 mm long, less than 1 mm wide, sparsely lepidote; disc patelliform, 0.5–1 mm long, 2–3 mm wide. Capsule linear, 50–65 cm long, 2–2.5 cm wide, strongly flattened, completely glabrous except for a few scattered lepidote scales, drying black or blackish, the midline not raised, the margins parallel; seeds thin, rectangular, essentially wingless, 2–2.1 cm long, 3–3.5 cm long, uniformly brownish or with the extreme margin subtranslucent, the linear hilum extending most of length of seed.

TYPE: PERU. LORETO: Province Maynas, Río Yaguasyacu, tributary of Río Ampiyacu, below Borro Indian village of Brillo Nueva, riverside forest, mostly seasonally inundated, liana, flowers deep yellow, calyx and bracts light green, tendril simple, 7 Nov. 1977, *Gentry & Revilla 20348* (MO, holotype; AMAZ, F, GH, MISSA, NY, USM, isotypes).

Widespread but very rarely collected in central and upper Amazonia.

Additional Collections Examined: PERU: LORETO: type locality, *Gentry & Revilla 20354* (AAU, AMAZ, F, INPA, MO, NY, US, USM). BRAZIL. PARÁ: Obidos, varzea perto do Amazonas, 25 Nov. 1910, *Ducke s.n.* (MG-11510).

This species is closest to *M. adenophora* Sandw. in its conspicuously pubescent leaves and spathaceous calyces subtended by foliaceous bracteoles. That species differs in having gland-tipped trichomes, the inflorescence and bracteoles villous, conspicuous foliaceous, pseudostipules, pubescent fruits, and the leaflets larger and becoming bullate and glabrescent with age.

Memora pseudopatula A. Gentry, sp. nov.

Frutex scandens, ramulis teretibus, sine lenticellis. Folia pinnata vel bipinnata, interdum cirrhis simplicibus; foliola anguste ovata vel elliptica, obtusa vel acuminata, quasi glabra. Calyx campanulatus, bilabiatus, minute puberulus; corolla tubulo-infundibuliformis, glabra; ovarium lineare, minute lepidotum, glandulosum; discus patelliformis. Capsula lineari-oblonga, aliquantum complanata, minute lepidota.

Liana; branchlets terete, finely striate, elenticellate, the nodes without interpetiolar glandular fields; pseudostipules small, thick-foliaceous. Leaves 2-foliolate to pinnate or bipinnate, most frequently ca. 6–11-foliolate, bifoliolate and biternate leaves often with a simple tendril; leaflets narrowly ovate to elliptic, obtuse (rarely retuse) to acuminate, basally rounded or obtuse, coriaceous to subcoriaceous, 5–27 cm long, 2–11 cm wide, usually with a few extremely short trichomes near the base of the midvein above, inconspicuously scattered lepidote below; petiole and petiolules glabrous or very inconspicuously puberulous at the joints. Inflorescence an axillary raceme, one per axil, distinctly minutely puberulous

with simple trichomes, the pedicels 3–10 mm long, the bracts small, subfoliaceous, ovate, 3–4 mm long, 2–3 mm wide, caducous, each flower subtended by a pair of ovate bracteoles 3–4 mm long and ca. ¼ as long as the calyx, attached ca. 1 mm below the base of the calyx, the bracts and bracteoles puberulous and with conspicuous plate-shaped glands. Flowers with the calyx coriaceous, campanulate, bilabiately split ca. ⅓ its length, 11–17 mm long, 7–12 mm wide, minutely puberulous, usually with plate-shaped glands in the upper half; corolla pure intense yellow, tubular-infundibuliform, 7–9.5 cm long, 1.8–3 cm wide at the mouth of the tube, the tube 6–7 cm long, the lobes 1–2 cm long, completely glabrous except inside at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 3–4 mm long, the filaments 2–3 cm long with insertion 1.8–2.5 cm from the base of the corolla tube; pistil 4–5 cm long, the ovary linear, 6–7 mm long, 1.5 mm wide, minutely lepidote and with scattered large round glands; disc patelliform-pulvinate, 1.5 mm long, 4–5 mm wide. Capsule linear-oblong, somewhat compressed, the apex rounded to bluntly acuminate, 20–22 cm long, 2.5–3.2 cm wide, the margins undulate, midline not evident, minutely lepidote and inconspicuously raised-glandular, drying uniformly black without lighter flecks; seeds fairly compressed, bialate, the brown wings not demarcated from the seed body.

TYPE: PERU. LORETO: Río Mazán, just above La Libertad, ca. 35 km above Mazán, seasonally inundated tahuampa forest, ca. 150 m, vine, flowers pure yellow, single immature fruit green, slightly convex, 10 July 1976, *Gentry & Revilla 16617* (MO, holotype; AMAZ, COL, F, INPA, NY, US, USM, isotypes).

Memora pseudopatula occurs in seasonally inundated tahuampa or varzea forests in upper Amazonia and the Orinoco where it allopatrically replaces closely related *M. schomburgkii* (DC.) Miers of lower and middle Amazonia and Guayana.

Additional Collections Examined: PERU. LORETO: Río Itaya near Palo Seco (ca. 40 river km above Iquitos), ca. 120 m, 20 Mar. 1977, *Gentry et al. 18518* (MO). Río Nanay across from Santa Clara (above Iquitos), 120 m, 20 Mar. 1977, *Gentry et al. 18518* (MO); same locality, 7 Apr. 1977, *Gentry et al. 19093* (MO). Quebrada Tamshiyacu, ca. 150 m, 5 Nov. 1977, *Gentry et al. 20333* (MO). Río Yavari, Emilia, ca. 120 m, 22 Nov. 1977, *Gentry & Revilla 20787* (MO). Río Yavari between Emilia and Brazilian village of Paumari (above Atalaia del Norte), 22 Nov. 1977, *Gentry & Revilla 20795* (MO). Río Yavari, across river from Brazilian village of Paumari, 23 Nov. 1977, *Gentry & Revilla 20815* (MO). Río Yavari, between Brazilian village of Paumari and Emilia, 100 m, 25 Nov. 1977, *Gentry & Revilla 20947* (MO). Río Yavari, caserío San José, 30 min. de Petropolis, 10 Sep. 1976, *Revilla 1354* (MO). Cerca a San Fernando, Río Yavari, 23 Jan. 1977, *Revilla 2246* (MO). 7 km SW of Iquitos, 9 Sep. 1972, *Croat 20042* (MO). Gamitanacocha, Río Mazán, 100–125 m, 18 Jan. 1935, *J. M. Schunke 78* (MO). Banks of Río Nanay, 100 m, *Woytkowski 5143* (MO). COLOMBIA. VAUPÉS: Río Vaupés, 2 mi upriver from Mitu, 1 Nov. 1976, *E. Davis 217* (MO). VENEZUELA. AMAZONAS: San Fernando de Atabapo, Lago Titi near the city, 110 m, 23 Mar. 1974, *Gentry & Tillet 10852* (MO, VEN). Río Orinoco, Caño Guacamayo between San Fernando de Atabapo and Santa Bárbara, 110 m, 25 Mar. 1974, *Gentry et al. 10912* (MO, VEN). Río Orinoco, Caño Pavon above junction with Río Atabapo, 25 Mar. 1974, *Gentry et al. 10905* (MO, VEN). BOLÍVAR: Río Parguaza, between mouth and El Carmen (90 km upstream), 80–110 m, *Wurdack & Monachino 41095* (NY).

This is the commonest species of *Memora* in Peruvian Amazonia. In fact, it is the commonest liana of the seasonally inundated tahuampa (varzea) forests around Iquitos, with a density of 8 individuals over 2.5 cm d.b.h. per 1,000 m^2. *Memora pseudopatula* is intermediate between *M. patula* Miers and *M. schom-*

burgkii and not very different from either of them. In the *Flora of Peru* the few available collections were assigned to both *M. patula* and *M. schomburgkii;* I included the Venezuelan collections under *M. patula* in the *Flora de Venezuela.* The most significant difference between *M. patula* and *M. pseudopatula* is the larger much more strongly compressed capsule of the former. *Memora patula* also differs in a glabrous often elongate inflorescence, and usually shorter more evenly truncate calyx. As here interpreted, wind-dispersed *M. patula* is restricted to the dry areas of northern Venezuela and Colombia. Both *M. pseudopatula* and *M. schomburgkii,* its other close relative, are water dispersed and the fruits of the two species are virtually indistinguishable. *Memora schomburgkii* differs in a spathaceously split calyx, reduced few-flowered inflorescence and smaller bracts and bracteoles. It is possible that collections from intermediate areas would prove *M. pseudopatula* and *M. schomburgkii* conspecific, but the available collections support recognition of different varzea species of *Memora* in upper and lower Amazonia.

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A NEW PERUVIAN *STYLOCERAS* (BUXACEAE): DISCOVERY OF A PHYTOGEOGRAPHICAL MISSING LINK[1]

Alwyn H. Gentry[2] and Robin Foster[3]

Abstract

A new species of *Styloceras* (Buxaceae), *S. brokawii* A. Gentry & R. Foster, is described from lowland Amazonian Peru. This is the first non-Andean species of the genus and provides significant new phytogeographical evidence as to the origins of this remarkable and isolated genus.

Styloceras brokawii A. Gentry & R. Foster, sp. nov.—Fig. 1.

Frutex dioecius. Folia alterna elliptica, acuta vel breviacuminata, ad basim acuta. Inflorescentia masculina spica axillaris, gracilis, floribus solitariis, distantibus, bracteatis, sessilibus, antheris ca. 14, sessilibus. Flores feminei solitarii, pedicellati, calyce 4–5-lobato, ovario puberulo, stigmatibus 2(–3) magnis. Fructus globosus, stigmatibus persistentibus.

Dioecious (rarely monoecious) shrub 2–6 m tall; branchlets angulate when young, becoming subterete, glabrous, striate. Leaves alternate, elliptic, the apex acute to short acuminate, acute to abruptly attenuate at the base, (7–)10–20 cm long, (3.5–)5–9(–10) cm wide, entire, somewhat 3-veined from above the base, 4–5 secondary nerves on each side, these plane above and prominulous below, tertiary veins obscure, glabrous, the petiole 1–3 cm long. Male inflorescence, axillary, pendant, spicate, slender, 2–6 cm long, the flowers rather distant, each flower subtended by a ciliate-margined ovate bract ca. 1 mm long, the flowers sessile, the anthers ca. 14, sessile, bilocular, 1.5–2 mm long, slightly curved. Female flowers solitary, pedicellate, the pedicel 7–9 mm long, glabrous, with several very inconspicuous minute bracts near the base, the calyx 4–5-lobed, the lobes triangular, reflexed, the corolla absent, the ovary subsessile, truncate, 2-parted, minutely puberulous, the apex prolonged into 2 (rarely 3) large divergent stigmas over 1 cm long, the tips recurved, yellow when fresh, the base of the stigmas slightly contracted into the ca. 2 mm long style. Fruit globose, fleshy, yellow, 2–3 cm in diameter, the 2 stigmas persistent as 2 subapical horns 1.8–2 cm long, their bases separated by 1–2 cm, tardily dehiscent to expose gelatinous material surrounding 2–3 dark blue seeds.

Type: Peru. madre de dios: Prov. Manu, forest behind Manu settlement, 350 m alt, shrub 3–5 m, male catkins white, dioecious, 4 Aug. 1973, *R. Foster, H. Brokaw & N. Brokaw 2474* (MO, holotype; F, isotype).

Additional Collections Examined: Peru. madre de dios: in forest behind Manu settlement, 4 Aug. 1973, *Foster et al. 2471* (F, MO). Shintuya, forest 1 km up small stream from Río Madre de Dios, 8 Aug. 1974, *Foster et al. 3118* (F). Río Alto Madre de Dios, halfway between Shintuya and Manu settlements, forest near chacra of Sr. Carpio, 10–11 Aug. 1974, *Foster et al. 3229* (F), *3249*

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FIGURE 1. *Styloceras brokawii* A. Gentry & R. Foster. Fruit and female flowers (*Gentry et al. 27222*).

(F). Parque Nacional del Manu, Río Manu, vicinity of Cocha Cashu Biological Station, 14 Sep. 1976, *Foster & Russell 5035* (F). Río Palotoa, tributary of Alto Madre de Dios, NW of Shintuya, called Río Pantiacolla on maps, 500 m, 26 Aug. 1978, *Foster & Terborgh 6712* (F). Cocha Cashu Camp, Manu National Park, trails 4, 5, and 9, 380 m, 21 Oct. 1979, *Gentry et al. 27070* (AMAZ, F, MO, USM). Across river from Cocha Cashu camp, Manu Park, 380–420 m, 23 Oct. 1979, *Gentry et al. 27185* (MO, USM), *27221* (MO, USM), *27222* (AMAZ, F, MO, USM).

The known range of *S. brokawii* is between 350 and 600 m in the shade of closed seasonally inundated forest and noninundated upland forest. It seems most abundant in intermediate areas of alluvial soil subject to rare inundations. At the type locality this species is abundant with up to 10–30 individuals per hectare. In other collection sites, individuals were at densities of one or less per hectare. Its peak of reproductive activity occurs during the drier months of July, August, and September when the forest is partially deciduous. Most full-size individuals were in reproductive condition at the time of collection, but plants in bud and with ripe fruit could be found at the same time. There appeared to be more male than female plants, and females were usually larger. One collection (*Gentry et al. 27222*) has a female flower at the base of the predominantly male inflorescence.

This species is named in honor of Howard P. Brokaw who found the plants from which the first specimens were made and in recognition of the contributions of him and his family to the cause of biological conservation in the neotropics.

There are only three accepted species of the remarkable and isolated genus *Styloceras* which is sometimes recognized as constituting a distinct family (Airy Shaw, 1966). *Styloceras brokawii* is most similar to *S. laurifolium* (Willd.) H.B.K. which ranges from central Peru to the Colombian and Venezuelan Andes. That species differs in a denser male inflorescence, glabrous ovary, and thicker

leaves with more prominent venation. *Styloceras kunthianum* Juss. of the upper Pastaza valley in Ecuador, which was erroneously synonymized with *S. laurifolium* in the *Flora of Peru*, differs in being monoecious with much shorter inflorescences. *Styloceras columnare* Müll.-Arg. of the Soratá area of Bolivia differs most notably in having the styles united into a basal column.

Styloceras is phytogeographically, as well as taxonomically, problematical, and *S. brokawii* provides important new phytogeographical insight. Buxaceae is an ancient, basically Laurasian group, and *Styloceras* is the only South American genus (one West Indian species of *Buxus* also reaches the Venezuelan coastal cordillera). Citing the traditional grouping of *Styloceras* and African *Notobuxus* (now usually merged with *Buxus*, Gentry, 1978) as tribe Stylocereae, Raven & Axelrod (1974) suggest that nevertheless the family already may have been present in West Gondwanaland in the Cretaceous when more or less direct migration between Africa and South America was still possible. All of the other species of *Styloceras* are found at much higher elevations and the restriction of such a putatively old and archaic genus as *Styloceras* to the geologically young Andes has seemed anomalous. The new species is the first non-Andean *Styloceras*, suggesting a possible reinterpretation of the genus as an old tropical lowland forest one which successfully invaded the upper slopes of the Andes relatively recently. This interpretation is also supported by arrival of *Styloceras* in the palynological record of the Colombian Cordillera Oriental only about 1.2 million years ago (van der Hammen, 1974), well after the establishment of suitable montane habitat in that region. On the basis of its phytogeography we predict that *S. brokawii* will prove the least advanced member of *Styloceras*, a prediction which would be borne out if contraction of the inflorescence and fusion of the style bases prove to be specialized characters as would be expected.

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FOUR NEW SPECIES OF *DIOSCOREA* FROM AMAZONIAN PERU[1]

By Franklin Ayala F.[2]

Abstract

Four new species of *Dioscorea* from northeastern Peru are described: *D. revillae* F. Ayala, *D. tamshiyacuensis* F. Ayala, *D. claytonii* F. Ayala, and *D. schunkei* F. Ayala & T. Clayton.

During a recent study of the genus *Dioscorea* L. in northeastern Peru (Ayala, 1979) the following four new species were discovered.

Dioscorea revillae F. Ayala, sp. nov.—Fig. 1.

Herba sinistrorsum volubilis ca. 1.7 mm vix crassa lineis 10 vel plus proxime nodos praedita; folia 7–10 cm longa, 3.5–4.0 cm lata, alternata, ovata vel ovata-lanceolata, apice acuta, basi acuta, margine integro; venae laterales 5 eis externissimis bifidis; petiolus gracilis basi dilatatus, 0.3–0.5 mm crassus, 4–4.8 cm longus; inflorescentia spiciformis axillaris, ramis nullis, 17–20 cm longa; flores luteo-virides solitarii, 2–3 mm longi, ca. 3.2 mm in diametro, bracteis duabus basi floris utriusque locatis; sepala oblonga, ca. 2.3 mm longa, ca. 0.8 mm lata, apice involuta apiculata, basi acuta; stamina 6, filamentis cuneatis vel crassis; antherae subglobosae, longitudinaliter dehiscentes.

Herbaceous vine; stem sinistrorse, 1.7 mm thick, somewhat tetragonal, with 10 or more transverse lines close to the nodes; leaves 7–10 cm long, 3.5–4.0 cm wide, alternate, ovate to ovate-lanceolate, acute at the base and apex, the margin entire, the nerves 5, the most external bifid; petiole slender, dilated at the base, 0.3–0.5 mm thick, 4–4.8 cm long; inflorescence a spike, axillary, unbranched, 17–20 cm long; flowers yellowish green, solitary, 2.3 mm long, 3.2 mm in diameter, with 2 bracts at the base of each flower; sepals oblong, 2.3 mm long, 0.8 mm wide, the apex involute, apiculate, acute at the base; stamens 6, longitudinally dehiscent, the anthers subglobose, the filament cuneate and thick.

Type: Peru. loreto: Provincia Maynas, Distrito Iquitos, boca del Río Nanay, 1 Nov. 1976, *Juan Revilla 1730* (AMAZ, holotype; F, MO, USM, isotypes).

This species is related to *Dioscorea paraguayensis* R. Knuth which was placed by Knuth (1924: 72) in subgenus *Helmia* (Knuth) Benth., section *Sphaerantha* Uline. It differs in having 5 nerves rather than 7. The petiole of *D. paraguayensis* is 2.5 cm long and the rachis of the inflorescence is 7 cm long and branched, while the petiole of the new species is 4.8 cm long with the rachis reaching 20 cm in length and unbranched.

Dioscorea tamshiyacuensis F. Ayala, sp. nov.—Fig. 2.

Herba volubilis caule gracili, 0.2–0.4 mm crasso, inermi, glabro, sinistrorsum volubili lenticellis violaceis ornato; folia integra glabra, elliptico-oblonga ad oblongo-lanceolata, acuminata, basi rotun-

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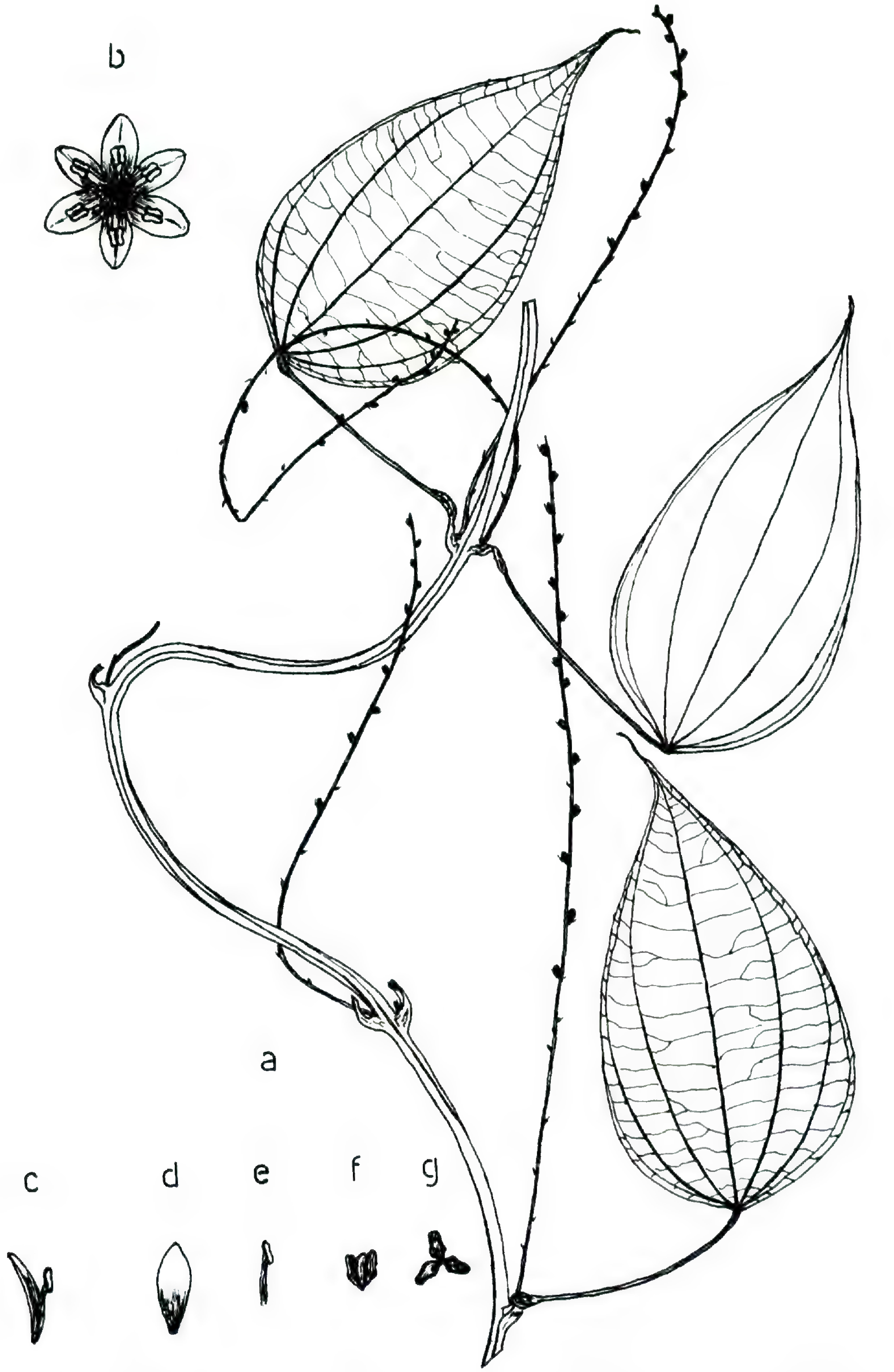

FIGURE 1. *Dioscorea revillae* F. Ayala.—A. Habit (×9/10).—B. Flower (×14).—C. Stamen adnate at base of petal (×14).—D. Petal (×14).—E. Stamen (×14).—F.–G. Torus (×14). [After *Revilla 1730* (AMAZ).]

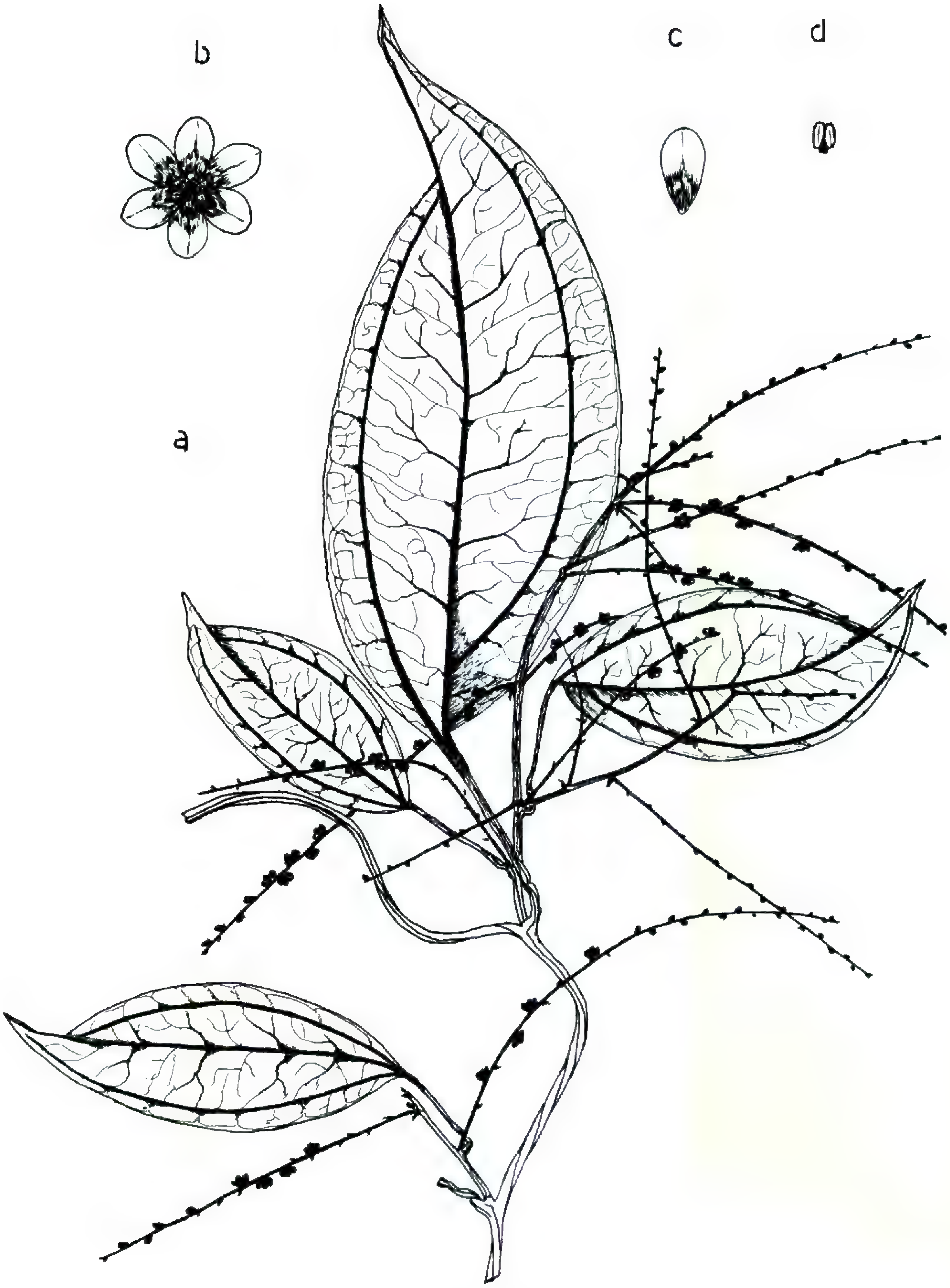

FIGURE 2. *Dioscorea tamshiyacuensis* F. Ayala.—A. Habit (×4/5).—B. Flower (×5 2/5).—C. Petal (×12).—D. Stamen (×15 1/5). [After *Ayala 564* (AMAZ).]

data, 9–11 cm longa, 4–5 cm lata, nervis 3, violaceis; petiolus 2–3 cm longus; inflorescentia spiciformis, fasciculata, rhachi diminuto-alata 12–20 cm longa; flores sessiles, 0.15–0.20 cm longi, 0.12–0.15 cm lati; sepala viridia ovato-lanceolata, 0.8–2 mm longa, 0.6–1 mm lata; petala violacea, ovata, introrsum volubilia, 1.0–2.5 mm longa, 1.0–1.2 mm lata; perianthium campanulato-rotundatum; stamina

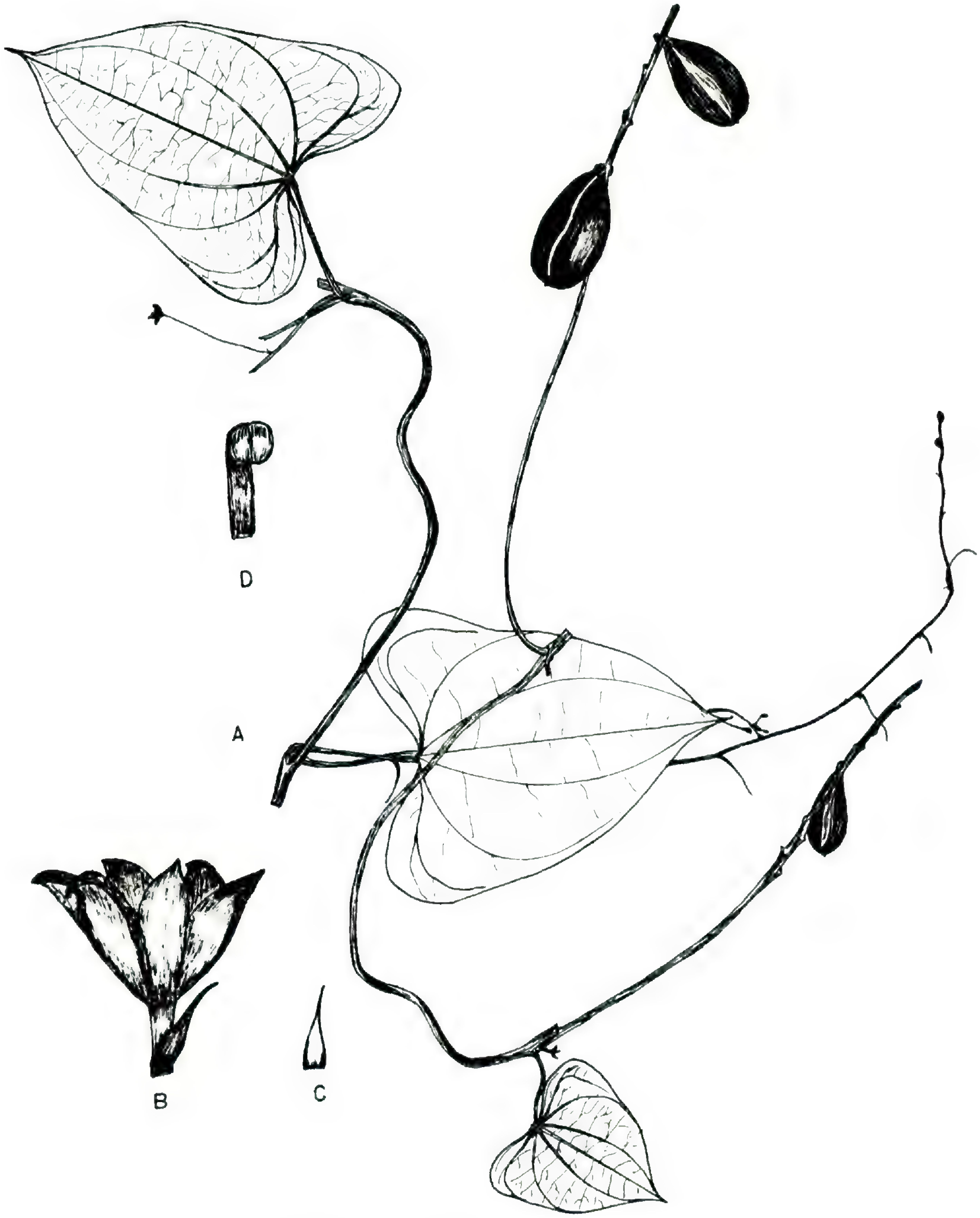

FIGURE 3. *Dioscorea claytonii* F. Ayala.—A. Habit (×¾).—B. Flower (×7½).—C. Bract (×4½).—D. Stamen (×15). [After *Klug 4345* (MO).]

6, antheris luteis, filamentis brevibus; flores bracteis duabus praediti, bractea utraque 0.1 mm longa, lanceolata vel ovato-lanceolata; radix lignosa.

Herbaceous vine; roots woody; stems slender, 0.3–0.4 mm thick, unarmed, glabrous, sinistrorse, with violet lenticels; leaves entire, glabrous, 9–11 cm long, 4–5 cm wide, elliptic-oblong to oblong-lanceolate, the apex acuminate, the base rounded, the nerves 3, violet; petiole 2–3 cm long; inflorescence a spike, fascic-

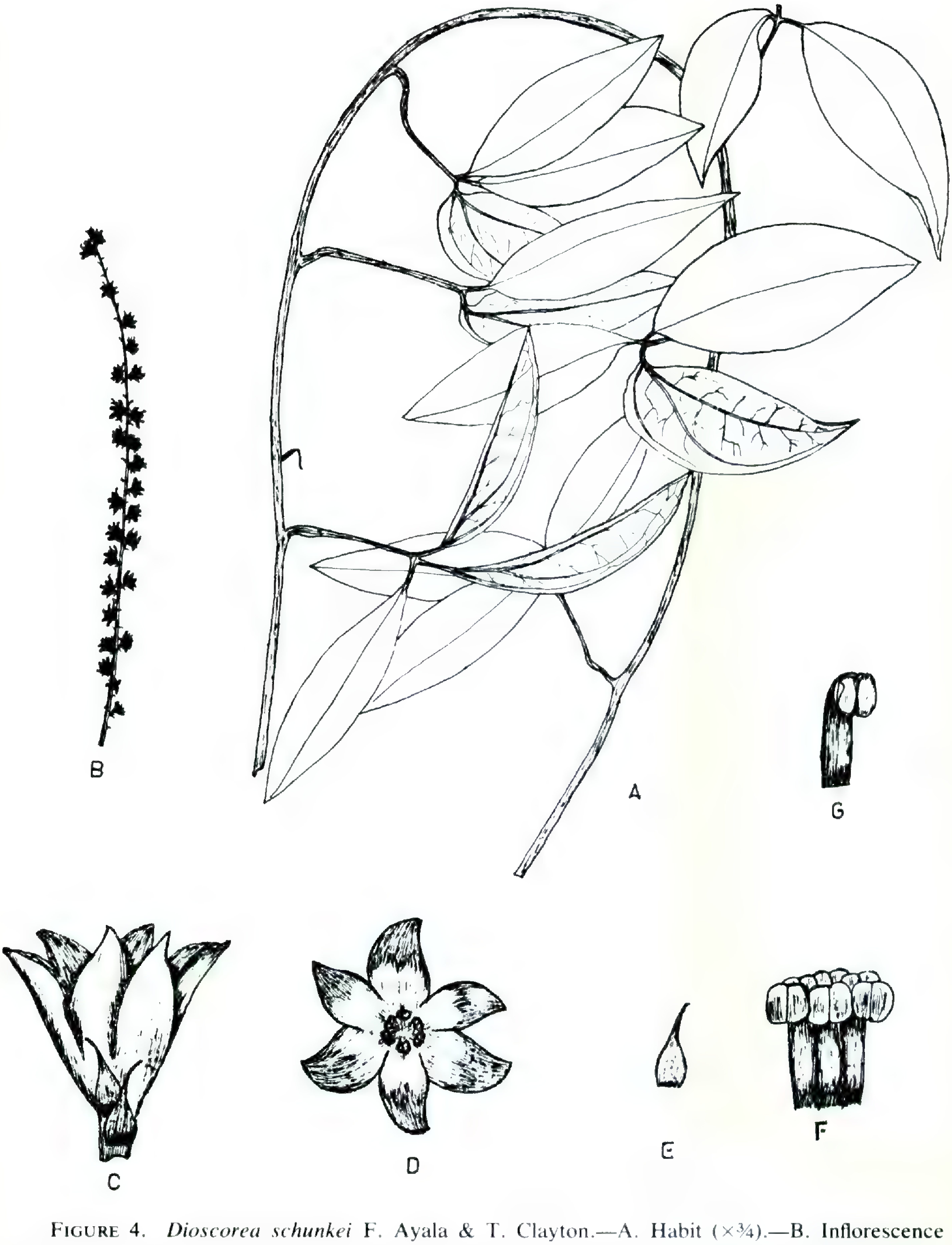

FIGURE 4. *Dioscorea schunkei* F. Ayala & T. Clayton.—A. Habit (×¾).—B. Inflorescence (×¾).—C.–D. Flower (×7½).—E. Bract (×4½).—F.–G. Stamen (×13). [After *Schunke 3825* (MO).]

ulate, the rachis minutely winged, 12–20 cm long; flowers sessile, 1.5–2.0 cm long, 1.2–1.5 cm wide, with 2 bracts at the base of each flower, the bracts 0.1 mm long, lanceolate to ovate-lanceolate; sepals green, ovate-lanceolate, 0.8–2 mm long, 0.6–1 mm wide; petals violet, ovate, introrse, 1–2.5 mm long, 1–1.2 mm wide; perianth campanulate-rotate; stamens 6, the anthers yellowish, the filaments short.

TYPE: PERU. LORETO: Provincia Maynas, Tamshiyacu, 8 Mar. 1974, *F. Ayala 564* (MO, holotype; AMAZ, isotype).

This species is related to *D. apurimacensis* R. Knuth which was placed by Knuth (1931: 94) in subgenus *Eudioscorea* Pax, section *Cryptantha* Uline. It differs from *D. apurimacensis* in twining sinistrorsely rather than dextrorsely and in having three nerves rather than five.

Dioscorea claytonii F. Ayala, sp. nov.—FIG. 3.

Herba dextrorsum volubilis, ca. 2.5–3 mm crassa, foliis alternatis, 9–11 cm remotis, cordiformibus, campylodromis; folia basi late cordata, apice acuminata, cuspidata, 2.5–7.5 cm longa, 2.3–5.5 cm lata, nervis 7–9, penultimis bifidis vel ramosis; petiolus glaber, 2–4 cm longus, 0.4 mm latus; inflorescentia axillaris, racemosa, rhachidi 6.5–8.0 cm longa, hirsuta; flores campanulati; perianthium 4 cm longum, 4.2 mm latum, pedicellus 1.2–2.8 cm longus, glaber; stamina fertilia 6, 1 mm longa, filamentis latis, 0.7 mm longis; anthera capitata, 0.3 mm longa; capsulae apice rotundatae, 2.0 cm longae, 1–1.3 cm latae; semina undique ala membranacea cincta, 0.2–0.5 cm longa, 0.2–0.3 cm lata.

Vine; stem dextrorse, 2.5–3 mm thick; leaves alternate, separated by 9–11 cm, cordiform, campylodromus, broadly cordate at the base, the apex acuminate or cuspidate, 2.5–7.5 cm long, 2.3–5.5 cm wide, with 7–9 nerves, the penultimate nerves bifid or branched; petiole glabrous, 2.0–4.0 cm long, 0.4 mm wide; inflorescence an axillary raceme, the rachis 6.5–8 cm long, hirsute; flowers campanulate, the perianth 4 mm long, 4.2 mm wide, the pedicel 1.2–2.8 cm long, glabrous; stamens 6, 1 mm long, the filaments broad, 0.7 mm long, the anthers capitate, 0.3 mm long; capsule apically rounded, 2 cm long, 1–1.3 cm wide, the seeds winged, 0.2–0.5 cm long, 0.2–0.3 cm wide.

TYPE: PERU. SAN MARTÍN: Provincia Mariscal Caceres, Distrito Juan Jui, Alto Río Huallaga, 400–800 m, forest, May 1936, *Klug 4345* (MO, holotype; phototype and fragm., AMAZ).

This species is related to *Dioscorea multispicata* R. Knuth which was described in subgenus *Helmia* (Knuth) Benth., section *Centrostemon* Griseb. (Knuth, 1916). It differs especially in having a long and broad filament rather than a short and thin one.

Dioscorea schunkei F. Ayala & T. Clayton, sp. nov.—FIG. 4.

Herba sinistrorsum volubilis, ca. 7–8 m alta, caule glabro, 2 mm lato; folia glabra, alternata, trifoliata, papyracea, segmentum foliatum oblongo-elliptica, apice acuta, basi attenuate acuta, 4–6 cm longa, 1.8–2.2 cm lata; petiolus 3 cm longus, 1 mm latus. Racemus rhachidi 9 mm longa; flores campanulati 4 mm lati, contorti, involuti; pedicellus 1 mm longus, bracteis duabus basi floris utrique locatis; bractea 1.2–2.5 mm longa, acuminata, caudata; stamina fertilia 6, 1.3 cm longa, 0.2 mm crassa, antheris 0.3 mm longis.

Vine, sinestrorse, 7–8 m high; stem glabrous, 2 mm wide; leaves glabrous, alternate, trifoliate, papyraceous, the leaflets oblong-elliptic, apically acute, acutely attenuate at the base, 4–6 cm long, 1.8–2.2 cm wide, the petiole 3 cm long, 1 mm wide; inflorescence a raceme, the rachis 9 cm long; flowers campanulate, 4 mm wide, contorted, involute, the peduncle 1 mm long with 2 bracts at the base, the bracts 1.2–2.5 mm long, acuminate, caudate; stamens 6, 1.3 mm long, 0.2 mm thick, the anthers 0.3 mm long.

TYPE: PERU, SAN MARTÍN: Provincia Marsical Caceres, Distrito Tocache Nuevo, en bosque alto camino a Shunte, 26 Feb. 1970, *J. Schunke Vigo 3825* (MO, holotype: photocopy and fragm., AMAZ).

This species is related to *Dioscorea trifoliata* H.B.K., placed by Knuth (1924) in section *Trifoliatae*. It differs in having hirsute leaves and six stamens rather than being glabrous and having three stamens.

The species was independently recognized as new by the late Temple Clayton of the University of Minnesota, as indicated by inclusion of his name as co-author.

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SYSTEMATICS, PHYLOGENY AND EVOLUTION OF *DIETES* (IRIDACEAE)[1]

PETER GOLDBLATT[2]

ABSTRACT

Dietes is a member of Iridaceae-Iridoideae and is probably the most primitive member of the Old World tribe Irideae. It shares characteristics of both *Iris* and the African genus *Moraea* and is most likely close to the ancestral stock that gave rise to these more specialized genera. *Dietes* comprises six species, five African and one remarkable disjunct on Lord Howe Island between Australia and New Zealand, *D. robinsoniana*. The South African *D. bicolor* appears more closely related to *D. robinsoniana* than to the other African species, and these two share several characters primitive in the genus. The remaining four African species include the wide-ranging *D. iridioides*, which extends from the southern Cape to Ethiopia, and three more localized eastern southern African species.

Dietes is a small genus of Iridaceae, closely allied to the African genus *Moraea* and to the widespread Northern Hemisphere genus *Iris*. Six species are currently recognized, five African and one restricted to Lord Lowe Island in the Tasman Sea between Australia and New Zealand (Fig. 1). In spite of the extraordinary disjunction in the distribution, there seems no doubt that *Dietes* is a natural genus, all the species sharing unique vegetative and floral structures and a basic chromosome number of $x = 10$.

HISTORY

The name *Dietes* was first proposed by R. A. Salisbury in 1812, but as published it was nomenclaturally invalid, lacking description or reference to a previously published generic description. Salisbury chose the name *Dietes* to indicate what he believed to be its dual affinities to both *Iris* and *Moraea*, a point of view fully supported here. Few authors accepted the genus initially, though Sweet (1830, 1839) put forward several combinations, unfortunately never validating the genus with a description. *Dietes* appears again in the literature in 1846 in an article by Spae concerning the species currently called *D. bicolor*. Spae used both *Moraea bicolor* and *Dietes bicolor* in the title, but apparently regarded *Moraea* as the correct generic name. Later, in 1852 when Spae again wrote about *D. bicolor*, he unambiguously placed it in *Moraea*.

Dietes was only fully accepted in 1866 by Klatt, who provided a complete generic description. Klatt acknowledged Salisbury as the source of the name and recognized three species in the genus, *D. bicolor*, *D. catenulata*, and *D. compressa*. The last two are, in my opinion, the same species and conspecific with the much earlier *D. iridioides*. It was also Klatt who realized that the newly described Australasian species *Iris robinsoniana* F. Muell. belonged in *Dietes* (Klatt, 1882).

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FIGURE 1. Worldwide range of *Dietes*, showing the distribution of the five African species in southern and eastern Africa and the single species on Lord Howe Island.

Salisbury was not the first to consider *Dietes* a distinct genus. Medikus in 1790 published *Naron* which, though confusingly described, is clearly a new genus accommodating only the Linnaean species *Moraea iridioides*, although under the superfluous name *N. orientale*. *Naron* was never accepted and apparently on only one occasion is the genus again mentioned, by Moench in 1794 where he proposed the corrected combination *N. iridiodeum* (L.) Moench. *Naron* was completely overlooked subsequently, although a perfectly valid earlier synonym for *Dietes*, even typified by the same species under a different name.

Dietes did not receive general acceptance during the nineteenth century, although Klatt (1882, 1895) continued to recognize the genus. Instead, J. G. Baker's view of *Dietes* as a subgenus of *Moraea* prevailed and the genus was so treated in the important works, *Flora Capensis* (Baker, 1896) and *Flora of Tropical Africa* (Baker, 1898). In 1928 Brown raised *Dietes* once more to generic rank,

and he described two new African species, *D. grandiflora* and *D. prolongata*, the latter now considered merely a minor variant of *D. iridioides*. From this time, *Dietes* was consistently recognized in southern Africa for the genus, as when Gerstner in 1943 described the Natal forest species *D. butcheriana*.

Brown (1928) was also responsible for changing the name of *D. iridioides* to *D. vegeta* based on *Moraea vegeta* L., a species dating from 1762 which he believed to be typified by the same figure that is the type of *M. irioides* L. (1767). As explained at length (Barnard & Goldblatt, 1975), this was incorrect. *Moraea vegeta* is in fact the type species of *Moraea* and is not a *Dietes*.

An important contribution to the understanding of *Dietes* was made by A. A. Obermeyer who, in a series of four beautifully illustrated articles in *Flowering Plants of Africa* (Obermeyer, 1967a, 1967b, 1968a, 1968b), reviewed current knowledge of *Dietes*. She contributed valuable new data on the biology of the genus based on her own observations and those of R. G. Strey, the Natal botanist. Obermeyer also described a new species, *D. flavida*, bringing the number of species in the genus to six.

Dietes is now widely known in many parts of the world as a horticultural subject. Although not the earliest name for the genus, *Dietes* is correct as it has been conserved against *Naron* (Goldblatt, 1973; Brummitt, 1978) in the interests of nomenclatural stability.

RELATIONSHIPS

Dietes is undoubtedly allied to both *Iris* and *Moraea*. Opinion has differed as to which of the two is more closely related, but there is perhaps a consensus that *Dietes* and *Moraea* are closer simply because both are Southern Hemisphere genera. I believe it may be closer to the truth to consider *Dietes* a primitive genus in the Iridioideae, and ancestral to *Moraea* and *Iris*. *Dietes* appears to me to have a combination of the more unspecialized features of both *Iris* and *Moraea*. It is an evergreen herb of areas with a fairly equable climate. It has a thick persistent rhizome, a fan of equitant, tough, long-lived leaves, and a freely branching scape which in *D. robinsoniana* and *D. bicolor* is paniclelike. The flower consists of free, spreading, clawed tepals; typically entirely free stamens (the filaments are joined basally in a form of *D. iridioides*); and flattened petaloid style branches each with the transverse stigmas and paired crests typical of both *Iris* and *Moraea*.

Iris differs in several respects: most species are deciduous; the inflorescence is usually reduced rather than freely branched; the perianth is usually united to form a tube; and the tepals are dimorphic with large pendant outer tepals and smaller, usually erect inner tepals. Important features shared with *Dietes* are: the rhizome, clearly primitive in *Iris*; the basically isobilateral leaf (specialized in some species and subgenera and square or bifacial); free stamens; and spathe valves free to base.

In *Moraea* the rootstock is always a corm, the leaf fundamentally bifacial (occasionally terete), and the deciduous condition is normal. In the flower, tepals may be subequal, but if so, both whorls are usually strongly reflexed (more often the inner tepals are smaller, sometimes erect, and occasionally lacking); a perianth tube is found in two species, but free tepals are basic to the genus; the

TABLE 1. Comparison of critical characteristics of *Dietes*, *Iris*, and *Moraea*.[a]

Character	Taxa		
	Dietes	*Iris*	*Moraea*
Evergreen	+	(+)−	−
Rhizome	+	+(−)	−
Free tepals	+	−	+(−)
Free stamens	+	+	−
Free spathe valves	+	+	(+)−
Isobilateral leaf	+	+(−)	−
Subequal tepals	+	−	+−

[a] The unspecialized condition of each organ is listed with presence indicated by plus, absence by minus. Exceptions, usually derived, are in parentheses.

filaments are always contiguous at the base and with minor exceptions partially united; and the spathe valves of the majority of species are united at least in the lower part.

The similarities and differences between *Dietes*, *Moraea*, and *Iris* are summarized in Table 1, where it is evident that *Iris* and *Dietes* share more unspecialized (i.e., primitive) features than do *Moraea* and *Dietes*. It seems reasonable, therefore, to consider *Dietes* ancestral to *Iris* and to *Moraea*, with *Moraea* on balance probably having diverged somewhat farther than *Iris* from the ancestral type. On this line of reasoning, *Dietes* emerges as the basal genus of Old World Iridoideae and close to the ancestral stock which gave rise to *Iris* and its allies in the Northern Hemisphere (*Hermodactylis*, *Belamcanda* and *Iris*-segregate genera *Iridodictyon*, *Juno*, *Xiphium*, etc.) and to *Ferraria*, *Moraea*, and its cormiferous allies in Africa (*Galaxia*, *Homeria*, *Hexaglottis*, *Gynandriris*, etc.). In an earlier article in which I proposed this hypothesis (Goldblatt, 1976), I suggested a classification in which these Old World Iridoideae be grouped in a single tribe Irideae, subdivided as follows: *Dietes*, *Iris*, *Hermodactylis*, and *Belamcanda* be grouped in one subtribe Iridinae; the corm-bearing, bifacial leafed *Moraea*, *Galaxia*, *Homeria*, *Hexaglottis*, and *Gynandriris* be placed in another, Homeriinae Goldbl.; and *Ferraria* with an isobilateral leaf and a distinctive type of corm in a third, Ferrariinae Goldbl. It seems to me this treatment reasonably, though not perfectly, reflects what is known to date about the relationships of the genera of Old World Iridoideae.

Dietes exhibits some similarities with two New World iridoid genera, *Neomarica* and *Trimezia*. These genera also comprise evergreen, mainly forest species, and the rootstock in *Neomarica* is a creeping, persistent rhizome. *Neomarica* and *Trimezia*, as well as several other bulb-bearing New World Iridoideae, have flattened, rather petallike style branches, though usually narrower and smaller than those in the Old World Iridoidea. The New World genera differ consistently in one significant feature, the inner tepals, often elaborately folded, are nectiferous. In contrast, Old World species have flat inner tepals which rarely produce nectar, a function here of the outer tepals. It seems logical to group all New World Iridoideae in one tribe, the earliest name for which would seem to be Tigridieae.

TABLE 2. Chromosome numbers in *Dietes*. New counts are indicated in bold type.

Species	Diploid Number	Reference or Collection Data
D. robinsoniana	20	Goldblatt (1979)
D. bicolor	40	Goldblatt (1971); Chimphamba (1974)
(as "*Moraea iridioides* var. *bicolor*")	40	Sharma & Sharma (1960)
	40	*Goldblatt 2884* (MO), South Africa, Cape, Kap R. valley.
D. iridioides	**20**	*Goldblatt 3732* (MO), South Africa, Cape, Swellendam distr.
(as *D. vegeta* (L.) N.E.Br.)	20	Goldblatt (1971) (three localities)
(as "*Moraea iridioides* var. *johnsonii*")	20	Sakai (1952); Sharma & Sharma (1960)
(as "*M. iridioides* var. *mcleyii*")	40	Sharma & Sharma (1960)
(as *D. prolongata* N.E.Br.)	20	Riley (1962)
(as *M. iridioides*)	20	Banerjee & Sharma (1971)
D. flavida	**20**	*Admiraal s.n.* (PRE), South Africa, Natal, Josini Dam.
D. grandiflora	20	Goldblatt (1971); Chimphamba (1974)
	20	*Bayliss 7014* (MO), South Africa, Cape, Riebeek East.
D. butcheriana	20	Goldblatt (1971)

CYTOLOGY

Basic chromosome number in *Dietes* is $x = 10$ (Table 2). Four of the five African species are diploid, $2n = 20$, while *D. bicolor* is tetraploid with $2n = 40$ (Goldblatt, 1971; Chimphamba, 1974). *Dietes robinsoniana*, counted from unvouchered seed obtained from the Royal Botanic Gardens, Kew, also has $2n = 20$, as does a hybrid *D. robinsoniana* × *D. iridioides* raised by M. Boussard, Verdun, France (Goldblatt, 1979). Evidently, one of the named cultivars of *Dietes*, *D. iridioides* "mcleyii" is polyploid, $2n = 40$ (Sharma & Sharma, 1960).

Karyotypes of all species are similar and comprise large metacentrics and submetacentrics and smaller acrocentrics. Size differences between matching pairs are small, and the range from largest to smallest is between 7 μm and 4 μm. Chromosome numbers in *Dietes* are listed in Table 2, which includes previously published data as well as the first report for *D. flavida*, and several original counts for species already known cytologically. Methods employed in obtaining counts have been described elsewhere (Goldblatt, 1978, 1979).

EVOLUTION

To summarize from the previous section, *Dietes* is seen as a primitive member of Iridoideae, and the most primitive genus of the Old World members of this subfamily. The species are all indigenous to equable habitats, either shady forest or forest margins, or along streams and other wet places. In Africa the genus is probably relatively ancient, probably dating back to Paleogene time, when the African climate was generally far more equable than it is at present. Extant species of *Dietes* are perhaps best viewed as relicts now restricted in distribution to well-watered habitats.

The single species on Lord Howe Island, which seems to be the most primitive in the genus, is clearly a relict, and is probably more like ancestral *Dietes* stock than is any living African species. Thus it probably has considerable antiquity on Lord Howe Island, a continental fragment that once had direct overland connections with Australia. It might be a relict of a once more widespread Australian group that has become extinct on the mainland. It is one of the puzzles of plant geography how *Dietes* reached Australasia, where it is the only member of the tribe Irideae. The most reasonable explanation seems to me long distance dispersal from Africa, probably well before the Pleistocene. In Paleogene time, when it seems likely that *Dietes* existed, Australia was well separated from Africa, but India occupied an intermediate position (Raven & Axelrod, 1974) and perhaps afforded a way-station for *Dietes*.

The evolution of *Iris* and its allies on the one hand and *Moraea* and its relatives on the other probably began in the mid-Oligocene as world climates began to deteriorate and habitats increased for strongly seasonal and deciduous forms like *Iris* and *Moraea*. The closure of the Tethys Sea in mid-Miocene time brought Africa-Arabia into contact with Eurasia, which would have greatly facilitated plant migration from Africa northward (Raven & Axelrod, 1978). It seems likely that the ancestors of *Iris* moved into Eurasia at about this time and began to spread and radiate from here throughout the Northern Hemisphere. By contrast, *Moraea* and its allies remained in Africa, sometimes growing near areas inhabited by *Dietes*, but always in drier habitats into which their dry-season dormancy allowed extensive radiation.

Evolution and Subgeneric Relationships

Within *Dietes* there seems to be one fundamental difference between the inflorescences of *D. robinsoniana* and *D. bicolor* compared with those of the remaining species. The inflorescence of *D. robinsoniana* with its much ramified paniclelike structure and large green bracts seems most likely to be closest to the ancestral and thus primitive type. *Dietes bicolor* is similar in inflorescence arrangement, but the plants and inflorescences are much smaller, the branching pattern more irregular, and the bracts smaller, and often dry. Occasionally branching may be suppressed in this species so that one or two upper nodes bear only a bract without an axillary branch.

The inflorescence of the other four species can in no way be called a panicle; the stem branches very irregularly, but bears several sheathing bracts along its upper length from the axils of which fertile branches, or stolons, may later be initiated. Occasionally stems may even be entirely unbranched, but sheathing bracts are always present indicating sites of suppressed, but potential, branching. It seems reasonable to consider this second type of inflorescence specialized by reduction from the panicle type in *D. robinsoniana* and *D. bicolor*.

A second character that unites *D. robinsoniana* and *D. bicolor* is the capsule which is similar in both, being globose in shape with a truncated, flat apex. The capsule of *D. bicolor* is much smaller, but in other respects very like that of *D. robinsoniana*. The capsules of the other species vary to some extent, but are generally elongated and tend to be oblong in shape. They seem more similar to

one another, despite differences in dehiscence, than to those of *D. robinsoniana* or *D. bicolor.*

It seems unreasonable to propose subgeneric divisions in so small a genus as *Dietes*, but it is important, I think, to emphasize the similarities between *D. robinsoniana* and *D. bicolor* relative to the other four species and to indicate their apparent primitive position in the genus. I propose an informal grouping, *Paniculatae*, for these two species and a second, *Pauciramosae*, for the remaining.

Among the *Pauciramosae*, a general morphological similarity in all vegetative and floral features suggests that the species of the group are closely related. They are probably of much more recent origin. The large flower of *D. grandiflora*, extending to stamens and style branches, sets this species somewhat apart, though the similarities of this streamside and open-woodland species to the forest-dwelling *D. iridioides* are many, and it is sometimes difficult to tell them apart from dried material. *Dietes butcheriana*, although distinct, appears to be a localized derivative of the less specialized *D. iridioides*, adapted to the mist forests of Natal. The localized and disjunct *D. flavida*, very difficult to distinguish from *D. iridioides*, appears also to have been derived from the more widespread *D. iridioides*, and is adapted to forest margin situations.

MORPHOLOGY

ROOTSTOCK

Dietes has a thick, tough, fibrous to woody creeping rhizome which persists for several years. It bears a fan of equitant leaves at its apex. Side branches are produced from lateral buds which grow eventually to form new plants, initially grouped in a clump with the original plant.

LEAVES

The leaves of *Dietes* are, like most Iridaceae, isobilateral, and linear to ensiform, and they are arranged in a distichous fan. The leaves are thick, leathery, and fairly long-lived so that plants are evergreen. Except in *D. bicolor*, there is no discrete central vein, although several large veins run together in the lower part of the leaf. In *D. bicolor* two or more large median veins generally run very close together, simulating in appearance a midvein. Leaflike structures without a free lamina are considered bracts and are discussed in the following section.

SCAPE

The flowering stem, or scape, simply referred to in the text as the stem, is erect, fairly thick, and usually as high or higher than the leaves. The stem bears leaves on the lower nodes which decrease in size upwards. Upper nodes bear bractlike leaves that are entirely sheathing and lack a lamina. They closely resemble the spathe valves of the inflorescence, except in *D. bicolor* in which the stem bracts are smaller and often dry.

The stem is usually branched in the upper part, either forming a distinct paniclelike inflorescence as in *D. robinsoniana* and *D. bicolor* (Fig. 4) or forming

an irregular, rather lax type of inflorescence (Fig. 5). In *D. iridioides* stems are sometimes unbranched, but typically only in young individuals. At all the branch points of the stem, the subtending stem bracts are paired, a feature apparently not usual in Iridaceae, but known also in *Pilansia* (Ixioideae) and *Bobartia* (Sisyrinchioideae) (Lewis, 1954).

INFLORESCENCE

The ultimate inflorescences of *Dietes* are the terminal, so-called rhipidia typical of Iridaceae. Two opposed bracts, called spathes, enclose a several-flowered inflorescence in which individual flowers are borne one by one several days or weeks apart. The flowers are raised on a stiff pedicel which is characteristically covered with a light brown pubescence on one side. This may be difficult to see in older flowers or in fruiting plants, but is present in all species. The spathes are herbaceous but stiff in texture, with the inner longer than the outer. The apices are obtuse to emarginate and usually turn brown in mature inflorescences. Individual rhipidia may be solitary, grouped in a lax arrangement, or together form a panicle as detailed in the section dealing with the stem.

FLOWERS

The flowers are generally *Iris*-like, large, pale colored, and usually have conspicuous nectar guides at the base of the limbs of the outer tepals. The tepals are free, unguiculate, and differentiated into a larger outer and smaller inner whorl. The claws of the tepals are ascending, and the limbs spread horizontally. The claws of the outer tepals have a basal nectary and a median line of pubescence (a beard), and they are usually spotted or striped yellow to orange. The inner tepals are seldom marked, but there are conspicuous brown marks on the claws of the inner tepals of *D. grandiflora* (Fig. 8).

ANDROECIUM

The three filaments are free except in forms of *D. iridioides* and are held apart from one another. They are slender with a slightly broadened base. The anthers, held against the style branches, are extrorse, shortly tailed, and have a small apical appendage. In the southern Cape forms of *D. iridioides* the filaments are joined in the lower half and have a bulbous base. In plants occurring to the east the broadened bases of the filaments are contiguous but free.

GYNOECIUM

The ovary is large, green, and typically exserted from the spathes, though partly included in *D. robinsoniana* and sometimes in *D. bicolor*. The style, itself slender and short, divides to form three large flattened petaloid branches opposite the outer tepals. Each style branch is inclined and lies against a tepal claw. The stigma is a transverse, single or bilobed membranous structure located near the top of the style branch. The style branch bifurcates above the stigma to form a pair of petaloid appendages called crests.

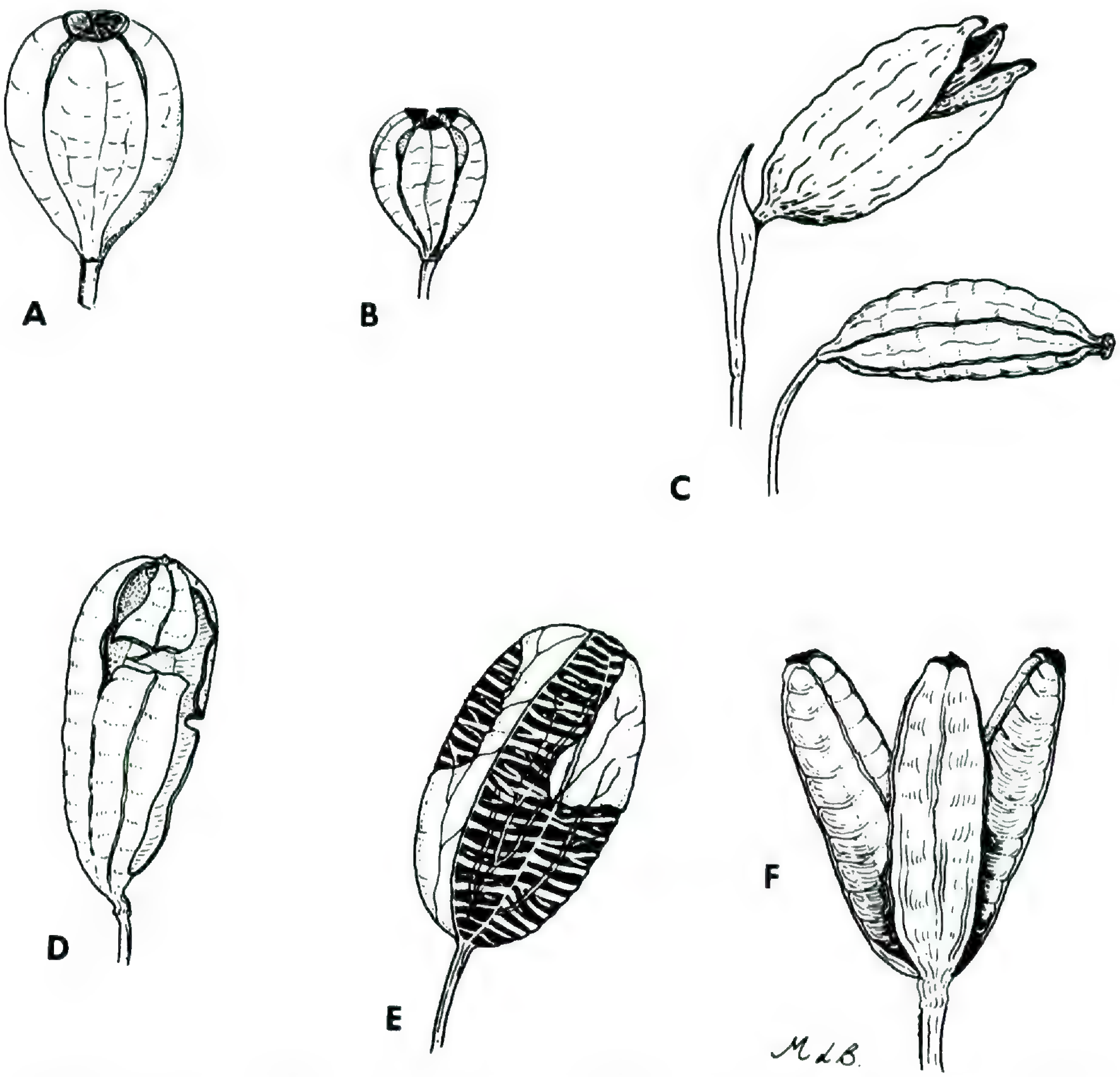

FIGURE 2. Ripe capsules of *Dietes*, all approximately life size.—A. *D. robinsoniana* (partially dehisced).—B. *D. bicolor*.—C. *D. iridioides* (dehiscent and indehiscent forms).—D. *D. flavida*.—E. *D. butcheriana*.—F. *D. grandiflora*.

FRUITS

The fruit is typically a loculicidally dehiscent capsule in *Dietes*. The degree of dehiscence varies, and fruits of *D. butcheriana* are indehiscent, while those of *D. flavida* split irregularly according to Obermeyer (1968b). The capsules are tough, thick-walled structures and are distinctive in each species (Fig. 2). In *D. robinsoniana* and *D. bicolor* the capsules are erect, globose, with a flat truncated apex and partially dehiscent from the apex to about the middle. In *D. grandiflora* and *D. iridioides* the capsules are oblong and ridged, and in the latter usually conspicuously rostrate. According to Obermeyer, the capsule of *D. grandiflora* is fully dehiscent, but in *D. iridioides* the capsules lie on the ground and decay but do not split. My own experience is contrary; I have observed *D. iridioides* in cultivation and in the field and have noted mature capsules splitting at least to the midline (Fig. 2B). Collections from the southern Cape also have partly de-

hiscent capsules. Most collections from elsewhere in Africa have capsules closed or split only near the apex, and it seems that there is some degree of variation in this character in *D. iridioides*. The capsules of *D. flavida* and *D. butcheriana* are distinctive in their smooth surface, somewhat globose rather than oblong shape, and in being pendulous (Figs. 2C–D).

SEEDS

Seeds of all species of *Dietes* are large, somewhat irregular in shape, and distinctly flattened.

SYSTEMATICS

Dietes Salisb. ex Klatt, Linnaea 34: 583. 1866, nom. cons. vs. *Naron* Medikus. TYPE SPECIES: *D. compressa* (L.f.) Klatt, nom. illeg. superf. pro *Moraea iridioides* L. = *Dietes iridioides* (L.) Klatt.

Naron Medikus, Hist. & Comment. Acad. Elect. Sci. Theod.-Palat. 6: 419. 1790, nom. rej. vs. *Dietes* Salisb. ex Klatt. 1866. TYPE SPECIES: *N. orientale* Medikus, nom. illeg. superf. pro *Moraea iridioides* L. = *Dietes iridioides* (L.) Klatt.
Dietes Salisb., Trans. Hort. Soc. London 1: 307. 1812, nom. nudum.
Moraea Miller sensu Linnaeus, Syst. Nat., ed. 12, 2: 78. 1767; sensu Miller, Gard. Dict., ed. 8. 1768 et sensu auct., pro parte.
Iris series *Dietes* Salisb. ex Baker, J. Linn. Soc. Bot. 16: 147. 1878. TYPE SPECIES: *I. compressa* L.f.
Moraea subgen. *Dietes* Salisb. ex Baker, Handb. Irid. 48. 1892; Fl. Cap. 6: 11. 1896. TYPE SPECIES: *M. iridioides* L.

Plants medium to large, perennial, evergreen, herbs. *Rootstock* a thick, fibrous creeping rhizome, persisting for several years. *Leaves* several, distichous at the apex of the rhizome, tough, leathery, equitant, linear to ensiform. *Stems* usually erect, bearing leaves at the lower nodes and sheathing spathelike bracts at the upper nodes; branching irregularly in the upper half or forming a distinct many-branched panicle; stem bracts paired at the branch points. *Inflorescences* enclosed in paired, opposed sheathing, bractlike spathes, the outer spathe smaller, the margins free to the base; flowers several per spathe, borne one at a time on stiff pedicels which are characteristically pubescent on the outer surface. *Flowers* large, pale colored with nectar guides at the base of the limb of the outer tepals, the claw of the outer tepal bearded to papillate in midline; *tepals* free to the base, the outer whorl larger, both whorls of tepals with an ascending claw and outspread limb. *Filaments* either free, filiform with a slightly expanded base or broad based and contiguous or united in the lower part; *anthers* linear, held against the style branches. *Ovary* green, terete, included or exserted from the spathes; *styles* short, dividing to form 3 branches, *style branches* large, flattened and petallike, bearing transverse stigma lobes on the abaxial face above which the branch bifurcates, forming paired crests. *Fruit* a many-seeded capsule, either indehiscent, or partly to entirely splitting along locule septa; seeds large, somewhat irregular in outline, but depressed. *Basic chromosome number*: $x = 10$.

Number of species: 6.

Distribution: forests, forest margins, and streamsides, east, central and southeast tropical Africa, coastal southern Africa, and Lord Howe Island, Australasia; Fig. 1.

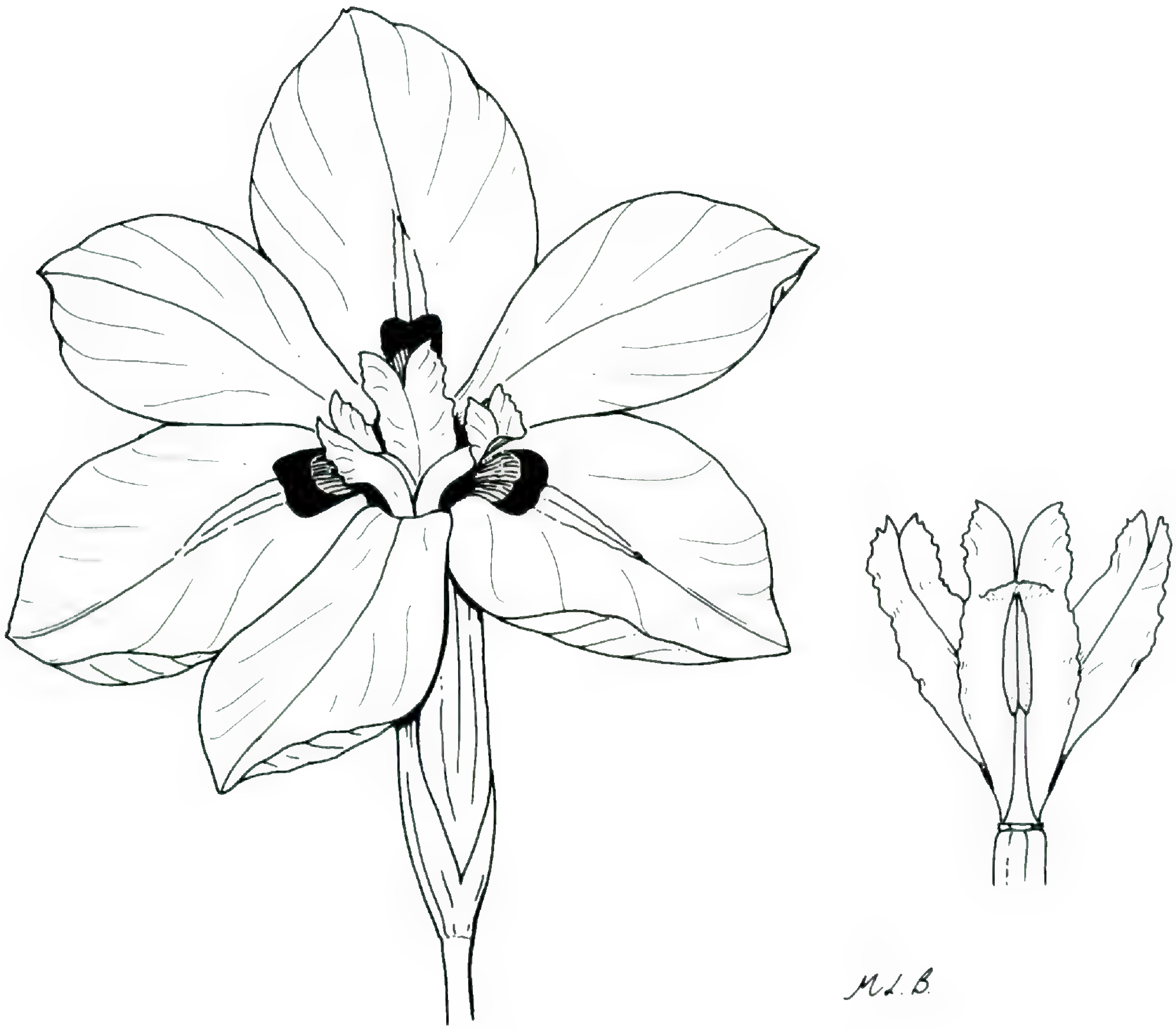

FIGURE 3. *Dietes robinsoniana*. Flower ×1; stamen and style branches ×2.

Artificial Key to *Dietes*

1. Leaves 30–50 mm or more at the widest point.
   2. Stem forming a regular branching panicle in the upper part; outer tepals ca. 45 mm long; stamens ca. 15 mm long .... 1. *D. robinsoniana*
   2′. Stem forming an irregularly branched inflorescence; outer tepals 30–32 mm long; stamens ca. 10 mm long .... 5. *D. butcheriana*

1′. Leaves less than 25 mm at the widest point.
   3. Stem bracts 9–20 mm long, often brown, obviously paired .... 2. *D. bicolor*
   3′. Stem bracts 25–50 mm long, usually green, not obviously paired and the inner much smaller, or evidently lacking.
      4. Outer tepals 45–60 mm long; style branches excluding crests 12–20 mm long; inner tepals with brown markings on the claw .... 6. *D. grandiflora*
      4′. Outer tepals 24–40 mm long; style branches 7–9 mm long; inner tepals not marked.
         5. Flowers white with a yellow nectar guide and blue to blue-flushed style branches; capsule erect, rough walled, usually furrowed and with a conspiduous beak (filaments sometimes united in the lower half) .... 3. *D. iridioides*
         5′. Flowers pale yellow with an orange brown nectar guide and yellow (occasionally blue-flushed) style branches; capsule pendant, smooth walled and without a beak (filaments always free) .... 4. *D. flavida*

Group PANICULATAE

1. Dietes robinsoniana (F. Muell.) Klatt, Erganz. (Abh. Naturf. Ges. Halle 15: 374. 1882) 40. 1882.—Fig. 3.

Iris robinsoniana F. Muell., Fragment. Phytogr. Austral. 7: 153, 1871. TYPE: Lord Howe Island, *Moore s.n.* (K, holotype).
Moraea robinsoniana (F. Muell.) Benth. & Muell., Fl. Austral. 6: 409. 1873.

Plants 1–1.5 m high. *Leaves* about as long as the inflorescences, linear-ensiform, the largest to 5 cm at the widest point. *Stem* erect, elliptical in section, to 15 mm thick, bearing small leaves at the lower nodes and spathelike bracts at the upper nodes; inflorescence much branched, forming the upper fifth of the stem, the nodes of the inflorescence with soft-textured, paired bracts, ranging in length from 5 cm at the lower to 2 cm at the upper nodes, the inner bract small, the outer inflated. *Spathes* 35–40 mm long, obtuse to emarginate, the outer ⅔–½ the inner. *Flowers* white with orange nectar guides on the outer tepals, opening ca. 10 A.M., fading in late afternoon; *outer tepals* 45 mm long, the claw ca. 15 mm long, the limb horizontal, ca. 30 mm wide; inner tepals slightly smaller. *Filaments* to 10 mm long; anthers 5–6 mm long. *Ovary* ca. 8 mm long, included in the spathes; *style* ca. 4 mm long, the branches ca. 10 mm long, ca. 8 mm wide; crests to 5 mm long, obtuse. *Capsule* globose, truncate at the apex, to 30 mm long, ca. 25 mm wide, dehiscent only in the upper half. *Chromosome number*: $2n = 20$.

Flowering time: spring and summer.
Distribution: forest and forest margins, Lord Howe Island, between Australia and New Zealand; Fig. 1.

I have noted in the earlier sections of this treatment that *Dietes robinsoniana*, the only non-African member of the genus, is correctly placed in *Dietes*. It seems to have, in fact, a combination of more unspecialized characteristics than any other species and is thus regarded as the most primitive in the genus. However, it is not altogether isolated and appears to be more closely related to the eastern South African *D. bicolor* than the latter is to the remaining African species.

2. Dietes bicolor (Steud.) Sweet ex Klatt, Linnaea 34: 584. 1863.—Fig. 4.

Moraea bicolor Steud., Nom. Bot., ed. 2, 2: 159. 1841. TYPE: South Africa, Cape, exact locality not known, illustr. in Bot. Reg. *tab. 1404*.
Iris bicolor Lindl., Bot. Reg. *tab. 1404*. 1831, hom. illeg. non Miller, Gard. Dict., ed. 8. Iris no. 13. 1768.
Dietes bicolor Sweet, Hort. Brit., ed. 3, 661. 1839, nom. inval. (*Dietes* nom. nudum).
Dietes bicolor Spae, Ann. Gand. 2: *tab. 70*. 1846, nom. inval. (not accepted by author).

Plants 80–120 cm high. *Leaves* 50–100 cm long, linear, pale green, with a distinct, usually double central vein, 6–12 mm wide. *Stem* erect, bearing short leaves on the lower nodes and short paired opposite bractlike structures on the upper nodes; stem bracts herbaceous or dry and brown, 9–20 mm long, acute, the margins free to the base. *Spathes* herbaceous, 34–45 mm long, the outer ½–⅓ the inner, the margins free to the base, the apices obtuse to emarginate. *Flowers* yellow, usually with a dark brown nectar guide on the outer tepals, the guide sometimes lacking and the tepal claw dotted; *outer tepals* 35 mm long, the claw ca. 12 mm long, bearded and speckled orange, the limb horizontal, to 23 mm

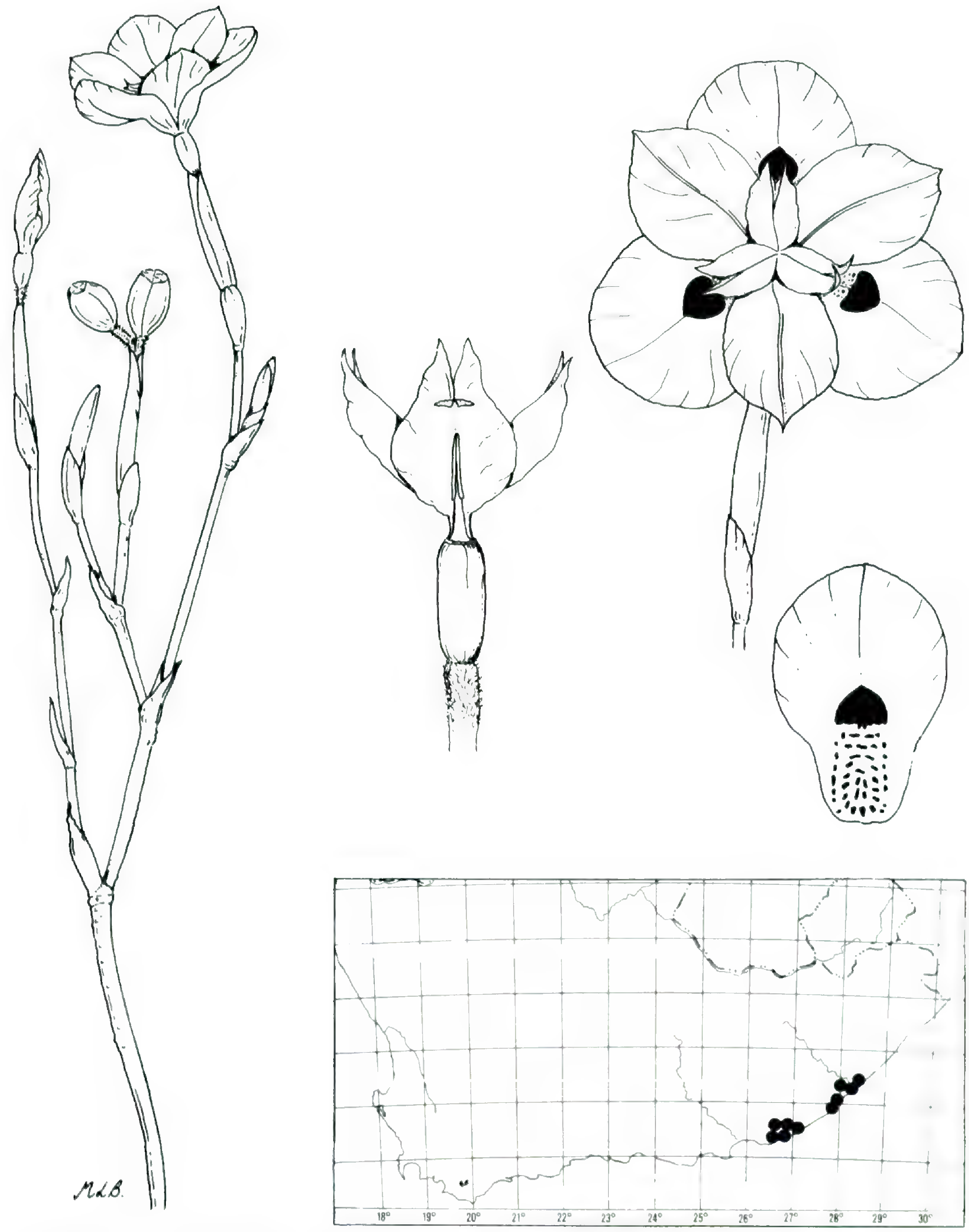

FIGURE 4. Morphology and distribution of *Dietes bicolor*. Flowering branch ×0.5; flower and outer tepal ×1; ovary, stamen and style branches ×1.5.

wide; inner tepals to 33 mm long, ca. 18 mm wide, horizontal. *Filaments* 6 mm long; anthers 4–8 mm long. *Ovary* ca. 10 mm long; *style* ca. 2 mm long, the branches 8–10 mm long, to 9 mm wide; crests ca. 5 mm long. *Capsule* to 25 mm long, globose-truncate, dehiscing only in the upper half. *Chromosome number* $2n = 40$.

Flowering time: spring–summer (Aug.–Feb.).

Distribution: along streams and vleis, the eastern Cape between Grahamstown and East London; Fig. 4.

Dietes bicolor, the only polyploid species of the genus, is seen as a relict, now confined to moist situations in a limited area of the eastern Cape, South Africa. It is taxonomically isolated and is almost certainly more closely related to the Lord Howe Island species, *D. robinsoniana,* than to any African species.

There has been some nomenclatural confusion over the authorship of the combination *Dietes bicolor* and over the original authority of the basionym. Lindley described *Iris bicolor* in 1831, but this name is illegitimate, being a later homonym. The epithet, used by Steudel in *Moraea* as *M. bicolor,* is considered valid only from this date (1841) when *M. bicolor* is considered a new name. Sweet's combination *D. bicolor* (1839) is invalid because *Dietes* was not at this time a validly described genus. Spae also used the name *D. bicolor* in 1846, but clearly did not accept this combination and instead appears to have regarded the name *Moraea bicolor* as correct for the species. *Dietes bicolor* is consequently only to be accepted from 1863 when Klatt provided a valid description for *Dietes,* and then made the combination accepted here.

Dietes bicolor is a valuable ornamental that is widely cultivated today. Plants may be very free flowering, and although each flower lasts only one day, plants usually produce flowers almost every day for months. Under unsuitable cultural conditions, *D. bicolor* may fail to bloom for years, while apparently healthy and producing foliage only.

3. Dietes iridioides (L.) Sweet ex Klatt, Th. Durand & Schinz, Consp. Fl. Afr. 5: 156. 1895.—Fig. 5.

Moraea iridioides L., Mant. Pl. 28. 1767. TYPE: South Africa, locality not known, cult. Chelsea Physic Gard., illustr. Miller, Fig. Pl. *tab. 238, fig. 1* (lectotype).

Naron iridioideum (L.) Moench, Meth. Pl. 627. 1794.

Dietes iridioides (L.) Sweet, Hort. Brit., ed. 2, 497. 1830, nom. inval. (*Dietes* nom. nudum).

Naron orientale Medikus, Hist. & Comment. Acad. Elect. Sci. Theod.-Palat. 6: 419. 1790, nom. illeg. superf. pro *Moraea iridioides* L.

Ferraria blanda Salisb., Prodr. 42, 1896, nom. illeg. superf. pro *M. iridioides* L.

Dietes iridifolia Salisb., Trans. Hort. Soc. London 1: 307. 1812, nom. inval. (*Dietes* nom. nudum) et superf. pro *Moraea iridioides* L.

Iris moraeoides Ker, Bot. Mag. sub *tab. 1407.* 1811, nom. nov. pro *Moraea iridioides* L.

I. compressa L.f., Suppl. Pl. 98. 1781; Thunb., Diss. Irid. no. 12. 1782. TYPE: South Africa, Cape, near Zeekorivier, *Thunberg s.n.* (Herb. Thunberg 1117 UPS, lectotype).

Dietes compressa (L.f.) Klatt, Linnaea 34: 584. 1863.

Moraea catenulata Lindl., Bot. Reg. *tab. 1074.* 1827. TYPE: Mauritius, R. Barclay, illustr. Bot. Reg. *tab. 1074* (lectotype).

Dietes catenulata (Lindl.) Sweet ex Klatt, Linnaea 34: 585. 1863.

D. catenulata (Lindl.) Sweet, Hort. Brit., ed. 2, 497. 1830, nom. inval. (*Dietes* nom. nudum).

Iris crassifolia Lodd., Bot. Cab. *tab. 1861.* 1832, nom. nudum.

I. crassifolia G. Don, Hort. Brit., ed. 3, 661. 1839, nom. nudum.

Moraea vegeta L. sensu Miller, Gard. Dict., ed. 8. 1768.

Dietes vegeta (L.) N. E. Br. sensu N. E. Br., J. Linn. Soc. Bot. 48: 36. 1928. =*M. vegeta* L.

Moraea iridioides var. *prolongata* Baker, Fl. Cap. 6: 26. 1896. TYPE: not cited but probably Natal, Inanda, *Wood 1341* (K).

Dietes prolongata (Baker) N. E. Br., J. Linn. Soc. Bot. 48: 37. 1928.

Dietes prolongata var. *galpinii* N. E. Br., J. Linn. Soc. Bot. 48: 37. 1928. TYPE: South Africa, Transvaal, near Barberton, *Galpin 1206* (K, lectotype).

FIGURE 5. Morphology and distribution of *Dietes iridioides*. Fruiting branch ×0.5; flower ×1; ovary, stamen and style branches ×1.5.

Plants (15–)30–60 cm high. *Leaves* 25–40(–60) mm long, 6–15(–25) mm wide, linear-ensiform. *Stem* bearing short leaves below, and sheathing, bractlike leaves above, irregularly branching; stem bracts 25–30 mm long, often dry and brownish; old inflorescences often producing long stolons which bear a fan of leaves distally that eventually root. *Spathes* 35–50(–55) mm long, the outer ca. ½ the inner, obtuse-emarginate at the apex. *Flowers* white with yellow nectar guides on the outer tepals, the claws of the outer and often the inner tepals orange dotted, the style branches blue or white, flushed with blue; *outer tepals* 24–35 mm long, the claw ca. 16 mm long, heavily ciliate in midline, papillate, the limb spreading to recurved, 12–16 mm wide; inner tepals 24–28 mm long, 9–12 mm wide, spreading-recurved. *Filaments* 5–9 mm long, free or united or contiguous in the lower 3 mm; anthers 3–6 mm long. *Ovary* 8–15 mm long, lightly ridged; *style* 2–3 mm long, the branches 7–9 mm long, 4–6 mm wide; crests ca. 5 mm long. *Capsule* ovoid-cylindric, usually rostrate, 20–30 mm long, 14 mm in diameter. *Chromosome number*: $2n = 20$.

Flowering time: sporadic during spring and summer, blooming earliest in areas of winter rainfall.

Distribution: evergreen forests, from the southern Cape near Riviersonderend throughout eastern southern Africa and northwards through Rhodesia, Malawi, Zambia, eastern Zaire, Tanzania, Uganda, to Kenya; Fig. 5.

Dietes iridioides is the most widespread and common species of the genus, extending almost from the southern tip of Africa to Kenya. It is easy to distinguish from related species by its relatively small white flower with violet style branches, and its rostrate, cylindrical capsule, which is frequently indehiscent. Following Obermeyer (1968a), I include as synonyms *D. prolongata*, a species recognized by N. E. Brown, as well as its variety, var. *galpinii*. The name *D. prolongata* was given to stolon-producing plants of *D. vegeta*, said to have unmarked outer petals. Stolon production is common in *D. iridioides* and may occur on any plant with old inflorescences.

Dietes iridioides was for several years known as *D. vegeta* (L.) N. E. Brown, following Brown's (1928) erroneous conclusion that Linnaeus's *Moraea vegeta* (1762) was to be typified by the illustration published in Miller's *Figures of Plants* (*tab. 238, fig. 1*), which is the type of *Moraea iridioides* (and thus of *D. iridioides* (1767). The reasons for Brown's error and the restoration of the name *D. iridioides* for the species have been described at length elsewhere (Barnard & Goldblatt, 1975). *Moraea vegeta* is the type species of *Moraea* and is currently regarded as the correct name for the Cape species also sometimes known as *M. tristis* (L.f.) Ker (Goldblatt, 1976).

There is an interesting pattern of variation in *D. iridioides*. Plants in the southern part of its range, in the southern Cape as far east as the Humansdorp district, have filaments united in the lower half. The filament column is distinctively swollen and bulbous towards the base. North and east of these populations, in the eastern Cape, essentially a summer rainfall area, plants have filaments with a similar bulbous base, but the individual filaments are free, but contiguous. I have seen few plants from the rest of the range, but other reports indicate that the filaments are narrower, with only slightly expanded bases, and they are en-

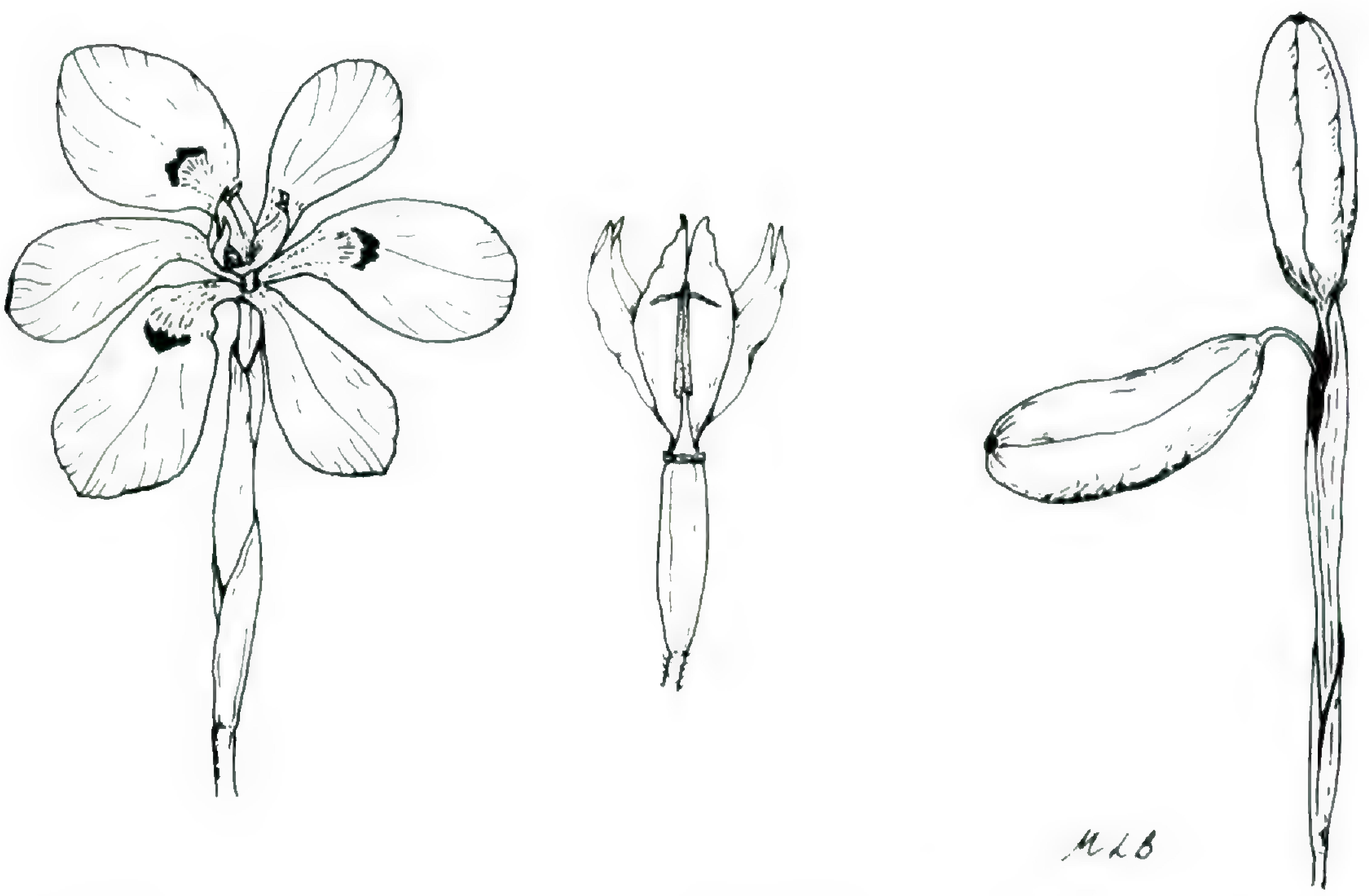

FIGURE 6. *Dietes flavida*. Flower and fruits ×1; ovary, stamen and style branches ×1.5.

tirely free. The pattern is apparently continuous. There seems no need to express this situation in a formal taxonomic way, but the condition of united filaments in the southern Cape plants indicates that they comprise a clearly recognizable form of *D. iridioides*.

4. **Dietes flavida** Obermeyer, Fl. Pl. Africa 149: *tab. 1488*. 1967. TYPE: South Africa, Natal, Jozini Dam, *Admiraal 5293* (PRE, holotype).—FIG. 6.

Plants 50–70 cm high. *Leaves* 30–50 cm long, linear-ensiform, 15–22 mm wide. *Stem* bearing leaves below and reduced sheathing spathelike leaves above; branching irregularly; stem bracts 30–50 mm long. *Spathes* (40–)45–50 mm long, the outer ca. ½ inner, the apices obtuse to emarginate. *Flowers* pale yellow, with brown nectar guides on the outer tepals and spotted on the claw; *outer tepals* 30–40 mm long, the claw ca. 15 mm long, the limb horizontal, 15–17 mm wide; inner tepals smaller, to 38 mm long. *Filaments* 4–6 mm long, broadened at the base; anthers 5–6 mm. *Ovary* 10–14 mm long; *style* 2–3 mm long, the branches ca. 8 mm long, 3–4 mm wide; crests 5–10 mm, acute. *Capsule* ovoid, pendulous, smooth, 30–35 mm long, ca. 12 mm in diameter, dehiscing irregularly. *Chromosome number*: $2n = 20$.

Flowering time: sporadically during the summer months.

Distribution: along forest margins and lightly shaded areas, Lebombo Mountains of northern Natal and Swaziland, also recorded from the Baviaans Kloof Mountains in the eastern Cape; Fig. 7.

Dietes flavida is closely related to the widespread *D. iridioides*, and is easily confused with this species. When living the two are readily distinguished by flower color as well as leaf characteristics. *Dietes flavida* has cream to yellow

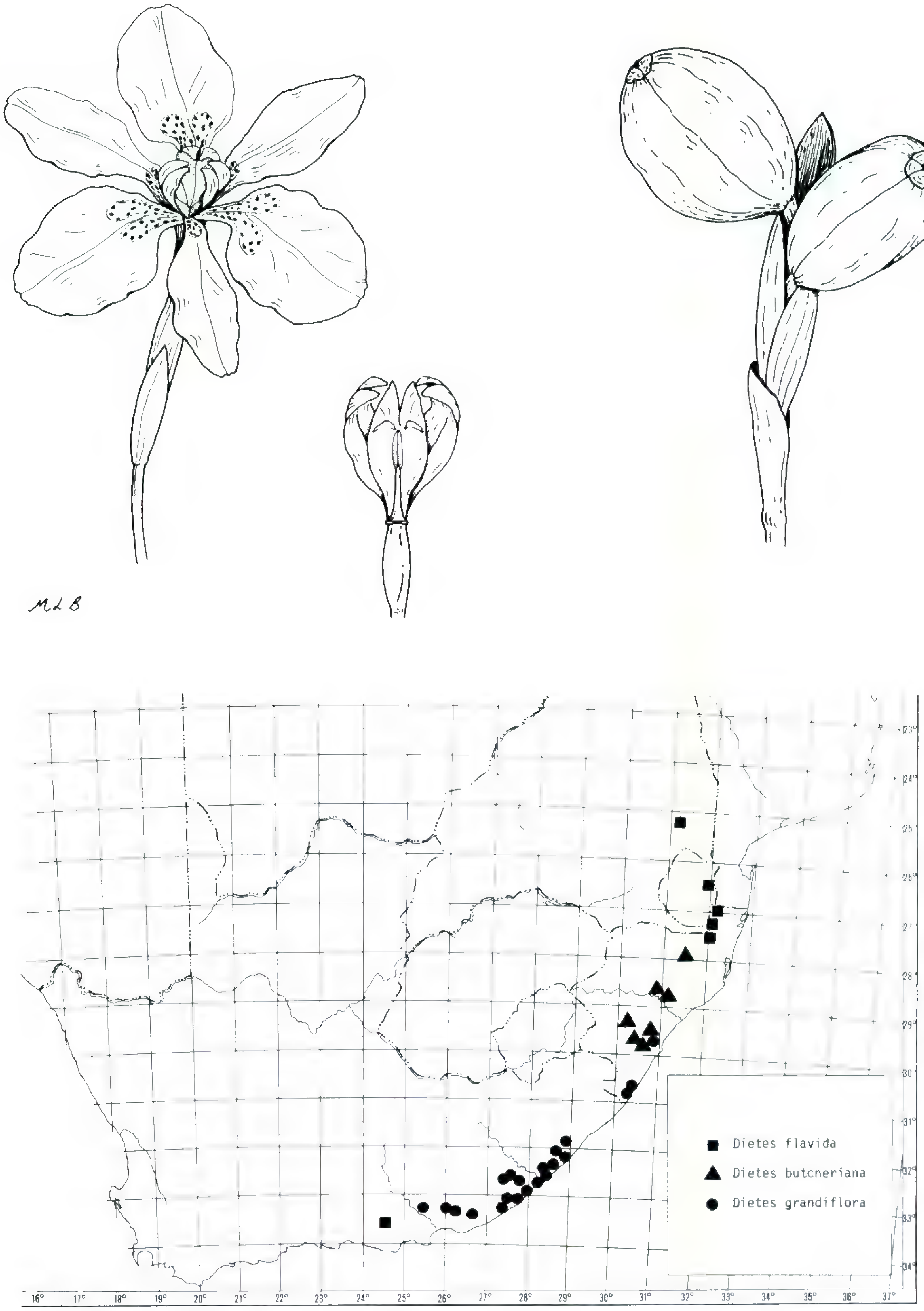

FIGURE 7. Morphology of *Dietes butcheriana*, and distribution of *D. butcheriana*, *D. flavida* and *D. grandiflora*. Flower and fruits ×1; ovary, stamen and style branches ×1.5.

flowers with brown-spotted nectar guides, the style branches are usually also cream or rarely very lightly flushed with purple, and the leaves have a grayish waxy covering. *Dietes iridioides*, in contrast, has white flowers with style branches conspicuously blue-purple flushed, and dark green leaves. When dry these

characters are lost, and fruits are needed for accurate determination. The fruits of *D. flavida* are oblong-ovoid, smooth, pendulous, and dehisce irregularly instead of along the carpel sutures. The fruits of *D. iridioides* are typically oblong and distinctly beaked, have a somewhat fissured surface, and are either indehiscent, or they split along the carpel sutures from the apex downwards for some distance.

Dietes flavida is characteristic of more open sites than the shade-loving *D. iridioides*, and it is reported to occur along forest edges, on cliffs, and along streams. When described by Obermeyer in 1967, *D. flavida* was thought to be restricted to the southern Lebombo Mountains in Natal and Swaziland. It has now been collected by R. D. Bayliss in the Baviaans Kloof Mountains of the southeastern Cape. This range disjunction is remarkable. Further collecting may bring to light some stations between these two extremes, but it is clear that this is nevertheless a true disjunction.

5. **Dietes butcheriana** Gerstner, J. S. African Bot. 9: 149. 1943. TYPES: South Africa, Natal, Nkandla Forest, Zululand, *Gerstner 601* (NH, lectotype); *Gerstner 4159* (NH, syntype); Obermeyer, Fl. Pl. Africa 149: *tab. 1487.* 1967.—FIG. 7.

Plants 50–120 cm high. *Leaves* larger than the stem, to 100(–120) cm long, ensiform, 30–48 mm wide. *Stem* thick, often somewhat flexuous, 50–60 cm long, with small leaves on the lower nodes and sheathing spathelike bracts on the upper nodes; stem bracts 30–60 mm long; branches relatively short. *Spathes* 45–60 mm long, the outer ca. ½ the inner, acute, obtuse or emarginate at the apex. *Flowers* white with yellow nectar guides on the outer tepals, the claws of the inner and outer tepals speckled orange, the style branches white; *outer tepals* 30–35 mm long, the claw 12 mm long, bearded, the limb spreading, 15–20 mm wide; inner tepals 25–35 mm long, to 12 mm wide, the limb spreading. *Filaments* 6 mm long; anthers 4–4.5 mm long. *Ovary* ca. 10 mm long; *style* ca. 3 mm long, the branches 8–9 mm long, 6–8 mm wide; crests 7–10 mm long. *Capsule* subglobose, 25–35 mm long, 20 mm in diameter, subpendulous, indehiscent, smooth when ripe. *Chromosome number*: $2n = 20$.

Flowering time: sporadic, mainly spring and summer.
Distribution: in deep shade, in mist-belt forests, Natal and Zululand; Fig. 7.

Dietes butcheriana, a Natal endemic of moist forest areas, is closely related to *D. iridioides* and may be regarded as a specialized derivative of this widespread African species. *Dietes butcheriana* can easily be distinguished by its very broad leaves, ca. 30–50 cm wide, white flowers without purple or blue-flushed style branches, and globose, smooth, indehiscent capsules.

6. **Dietes grandiflora** N. E. Br., J. Linn. Soc. Bot. 48: 35. 1928. TYPE: South Africa, Cape, Kentani Div., *Pegler 484* (K, lectotype; BOL, isolectotype).—FIG. 8.

Plants tall, 1–1.5 m high. *Leaves* 75–100 mm long, linear, 10–15(–20) mm wide. *Stem* branched irregularly, bearing short leaves at the lower nodes and spathelike bracts from the upper nodes; stem bracts 25–50 mm long, entirely

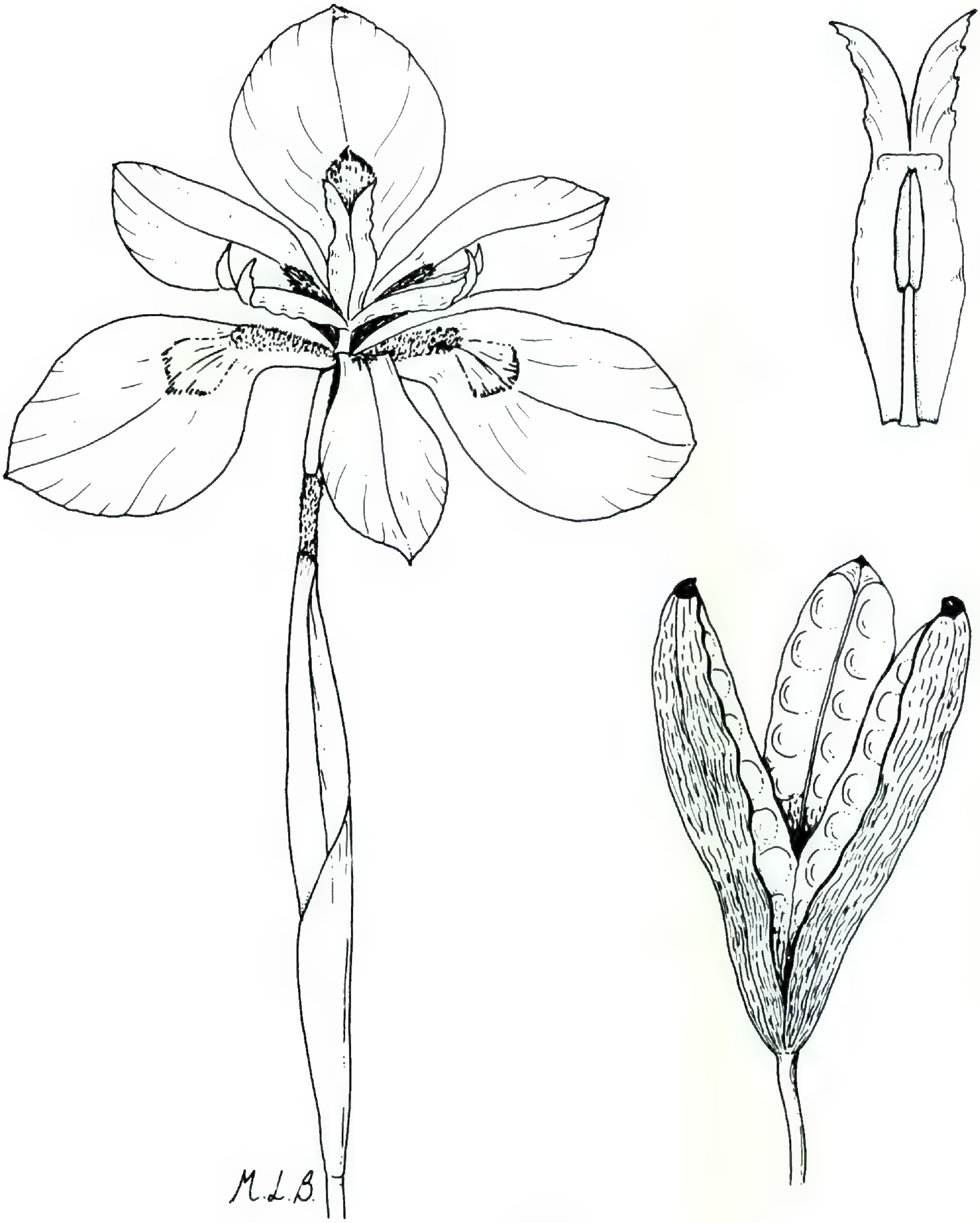

FIGURE 8. *Dietes grandiflora*. Flower ×1; stamen and style branches ×2; fruit ×2.

sheathing, herbaceous, the apices obtuse apiculate. *Spathes* 50–80 mm long, the outer about ½ the inner, the margins free to the base, the apices obtuse or emarginate. *Flowers* white with yellow nectar guides and a yellow beard on the outer tepals, the inner tepals marked dark brown towards the base, the style branches pale mauve; *outer tepals* 45–60 mm long, the claw 20–26 mm long, with a dense yellow beard down the midline, the limb horizontal to recurved, 25–35 mm wide; inner tepals (36–)40–45 mm long, to 25 mm wide, the limb spread

horizontally. *Filaments* 10–13 mm long, tapering from a broad base to the apex, contiguous at the base; anthers 7–10 mm long. *Ovary* 13–16 mm long; *style* ca. 5 mm long, the branches 12–20 mm long, 6–8 mm wide; crests 12–15 mm long, erect. *Capsule* 28–45(–50) mm long, ridged and furrowed vertically, cylindrical. *Chromosome number* $2n = 20$.

Flowering time: sporadic, during spring and summer.

Distribution: forest margins and especially along streams, the Eastern Cape from King William's Town through the Transkei to Natal; Fig. 7.

Dietes grandiflora stands out as the largest-flowered species of the genus. It is related to the more widespread *D. iridioides* but is easily distinguishable by its height and large flowers, which last three days in contrast to those of *D. iridioides* which last a single day. The flowers of *D. grandiflora* are conspicuously marked with a heavy yellow beard on the claws of the outer tepals, while the inner tepals have dark brown markings. This species is widely cultivated in areas of tropical to subtropical climates, and it will stand light frost. Once established, the plants are extremely persistent even when completely neglected. However, more and larger flowers and a longer flowering season reward those who give the plant better care.

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ADDITIONS TO THE ERICACEAE OF PANAMA[1]

ROBERT L. WILBUR[2] AND JAMES L. LUTEYN[3]

ABSTRACT

The following taxa of Ericaceae are newly described from Panama: *Cavendishia aberrans* Luteyn, *C. arizonensis* Luteyn, *C. chiriquiensis* var. *bullata* Luteyn, *C. fortunensis* Luteyn, *Didonica panamensis* Luteyn & Wilbur, *Disterigma hammelii* Wilbur & Luteyn, *Lateropora tubulifera* Wilbur & Luteyn, *Macleania megabracteata* Wilbur & Luteyn and *Themistoclesia revoluta* Wilbur & Luteyn. *Cavendishia quereme* (H.B.K.) Bentham & Hooker is reported for the first time from Panama, being previously known only from Costa Rica and Colombia. *Vaccinium dissimile* Blake is now known from Colón Province and the range of *Vaccinium jefense* Luteyn & Wilbur is extended to include Coclé Province. Keys to the Central American representatives of the genera *Disterigma*, *Lateropora*, and *Themistoclesia* are provided.

It may be surprising to many that, although an account of the Ericaceae of Panama was published only recently (Wilbur & Luteyn, 1978) based upon a study of all collections available in the American herbaria with significant holdings of Panamanian plants, a paper would be published so soon increasing by 15% the known ericad flora of that small county. All of these additions are based upon collections previously unavailable to us, and almost all are from collections made in only recently explored areas. It is safe to predict that many additional species await discovery in the extensive areas of Panama that are botanically either unexplored or little explored, and it is to be hoped that funds for continued exploration will be forthcoming. Obviously the botanical exploration of this biogeographically critical area is far from completed.

Cavendishia aberrans Luteyn, sp. nov.

Frutex epiphyticus. Folia ovato-lanceolata, 13–15 cm longa, 4.5–6 cm lata; petioli 15–17 mm longi. Inflorescentia racemosa, floribus 20; rhachides 12 cm longae; bracteae florales oblongae, 7–10 mm longae; pedicelli 19–20 mm longi. Calyx 6–7 mm longus; lobi calycis 1 mm longi calloso-incrassati. Corolla 41–43 mm longa. Stamina 34–36 mm longa, filamentis alternatim 1–2 mm et 5–6 mm longis, antheris tubulis inclusis alternatim 29–30 mm et 33–35 mm longis, poris 3 mm longis.

Epiphytic *shrub*; mature branches subterete, bluntly angled, glabrous, brown when dry. *Leaves* ovate-lanceolate, 13–15 cm long, 4.5–6 cm broad, basally obtuse, apically long but broadly acuminate, tan or olive brown when dry, glabrous, the margins slightly revolute, 3-plinerved, the nerves arising from the base, the midrib impressed above and raised beneath, the lateral veins plane above and raised beneath, the veinlets reticulate and slightly raised on both surfaces; petioles subterete, rugose, 15–17 mm long, 2.5 mm in diameter, glabrous, glaucous. *Inflorescence* viscid, 20-flowered, the lowest 3–4 floral bracts sterile; rachis 12 cm long, 3.5 mm in diameter at the base, bluntly angled, glabrous but with scattered

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globular glands; floral bracts conspicuously striate, oblong, basally truncate, apically rounded, 7–10 mm long, 5–6 mm broad, each margin with 10–20 angular or globular sessile glands, some of these often caducous; pedicels subterete, glabrous, 19–20 mm long, 1–1.2 mm in diameter, "purple," provided at the distal tip with 6–8 flesh-colored ovoid-angular short-stipitate glands each less than 0.5 mm in diameter; bracteoles continuous (not articulate) with the pedicel, subopposite, ovate, 1.5 mm long, ca. 1 mm broad at the base, the margins completely callose thickened. *Flowers* with the calyx glabrous, 6–7 mm long, the hypanthium 2 mm long, capanulate, 5 (weakly 10)-ribbed, basally apophysate with the rim undulate or turned upward, "purple," the limb spreading, noticeably constricted at the base, "green," 3–4 mm long, the lobes triangular, obtuse, 1 mm long, ca. 3 mm wide at the base, erect after anthesis, completely callose thickened without and onto the limb, only the margins callose thickened within, the sinuses flat or broadly rounded; corolla glabrous, 41–43 mm long, 6 mm in diameter, "waxy red," the lobes triangular, obtuse, 2 mm long; stamens of equal length overall, 34–36 mm long, the filaments pilose along the margins and inner surfaces, alternately 1–2 mm and 5–6 mm long, the anthers including the tubules alternately 29–30 mm and 33–35 mm long, the thecae 5–6 mm and 6–6.5 mm long, the tubules apically dehiscent by short clefts ca. 3 mm long with ragged and slightly flaring margins; style sigmoid, glabrous, 42–45 mm long. *Berry* not seen.

TYPE: PANAMA. COCLÉ: Near saw mill 8 km N of El Copé, 28 km NW of Penonomé, very wet cloud forest, 600–750 m, 9 Jan. 1977, *Maas, Berg & Dressler 2774* (U, holotype, photo NY).

Cavendishia aberrans is isolated within the genus, differing from all other species by its extremely long anther tubules and short dehiscence clefts. Species of *Cavendishia* usually have anther tubules and thecae of approximately equal length; however, the new species has tubules six times longer than the thecae. Also, species of *Cavendishia* normally have dehiscence clefts about half the tubule length; the new species has clefts only 3 mm long, being $^1/_8$–$^1/_9$ the length of the tubules.

In the long tubules in relation to the thecae and short dehiscence clefts, *Cavendishia aberrans* resembles the genus *Plutarchia* A. C. Smith, an Andean genus of Colombia, which may thus strengthen an already suspected relationship between these genera. Species of *Plutarchia* may have filaments of alternate lengths, although only slightly unequal, and floral bracts which reach 10 mm, thus superficially resembling *Cavendishia*. However, the floral bracts of *Plutarchia* are never showy. *Plutarchia* also differs in consistently smaller leaves (with only one exception leaves are less than 5 cm long); calyx hypanthia which are often angled or winged (never in *Cavendishia*) and never apophysate (common in *Cavendishia*); and most important, in the lack of development of the various types of glands on the calyces and bracts of so many cavendishias.

Cavendishia arizonensis Luteyn, sp. nov.

Folia elliptica, ovato-elliptica vel obovata, 7–13.5 cm longa, 2–6 cm lata, bullata; petioli 7 mm longi. Inflorescentia racemosa, floribus 82; rhachides 27 cm longae; bracteae florales oblongae, 17–22 mm longae; pedicelli 12–15 mm longi. Calyx glaber, hypanthio dense glanduloso, nonapophysato;

limbus campanulatus, lobis calloso-incrassatis et glandulosis secus margines inclusis 3.5–4 mm longus. Corolla immatura.

Shrub; mature branches subterete, striate, glabrous, yellowish brown when dry, with minute, black stipitate, globular glands ca. 0.1 mm in diameter. *Leaves* elliptic, ovate-elliptic to sometimes obovate, 7–13.5 cm long, 2–6 cm broad, basally cuneate, apically acute or short acuminate, olive brown above and tan beneath when dry, glabrous but with scattered, elevated, reddish globular glands 0.1 mm in diameter along the upper surface, and scattered red glandular fimbriae on the lower surface, 5-plinerved, the veins all arising from the base, the midrib and lateral nerves deeply and conspicuously impressed above, raised beneath causing the leaves to be longitudinally compressed and bullate, the veinlets impressed above, raised beneath; petioles subterete, flattened above, rugose, ca. 7 mm long, 4 mm in diameter, glabrous. *Inflorescence* racemose, viscid, 82-flowered; rachis subterete, bluntly angled, glabrous, 27 cm long, 6 mm in diameter at the base, the proximal 9–10 cm densely provided with globular glands, the distal portion without glands; floral bracts glabrous, oblong, 17–22 mm long, ca. 11 mm broad, basally clasping, apically rounded, marginally with a few globular glands; pedicels subterete, bluntly angled or striate, glabrous, 12–15 mm long, 1.5–2 mm in diameter, with scattered globular glands 0.2–0.3 mm in diameter, especially at the distal tip; bracteoles basal, broadly ovate, ca. 4 mm long, 3.5 mm broad, marginally glandular callose-thickened at the distal tip and flanked by oblong callose thickenings on each side (not globular glands). *Flowers* with the calyx glabrous, viscid, 6–6.5 mm long, the hypanthium cylindric, rugose, 2.5 mm long, basally nonapophysate, covered by globular, angular glands to 0.5 mm in diameter, the limb campanulate, 3.5–4 mm long including the lobes, without glands, the lobes triangular, 1.5 mm long, marginally glandular callose-thickened, the sinuses broadly rounded; corolla immature, cylindric, 18 mm long, 5–6 mm in diameter, "lavender," pilose, the distal third especially dense near the tip; stamens equal, 16 mm long, the filaments distinct, alternately 2 mm and 5 mm long, short pilose on the ventral side of the distal half, the anthers including the tubules alternately 12 mm and 15 mm long, the thecae 6 mm long, the dehiscence clefts 5 mm long; style 17 mm long. *Berry* not seen.

TYPE: PANAMA. VERAGUAS: N of Santa Fé, summit of Cerro Arizona, heath-like terrain formed by the dense crowns of elfin forest trees, 4700 ft, 10 Sep. 1978, *Hammel 4733* (MO, holotype).

In Wilbur & Luteyn (1978) *Cavendishia arizonensis* keys to *C. panamensis* to which it is most closely related. However, the differences, in combination, make the new species a very distinctive plant. *Cavendishia arizonensis* has a longer rachis (27 cm vs. 8–17 cm) with many more flowers (82 vs. 11–37); shorter floral bracts (17–22 mm vs. 20–50 mm), pedicels (10–15 mm vs. 11–19 mm) and corollas (18–20 mm vs. 25–35 mm); bracteoles with callose-thickened glands (not globular glands); and leaves which are strikingly bullate and have short acute tips (not flat and long acuminate to caudate-acuminate). Also, in *C. panamensis*, the floral bracts are proportionally longer covering the pedicels, calyx and lower half of the corolla at anthesis, whereas they cover only the pedicels and calyx in the new species. One other interesting note about the new species is that the inflo-

rescence and especially the calyces are covered by dead ants or ant-body parts. This is probably the result of ants being attracted to the glandular exudate (for feeding purposes?) and then getting stuck and being unable to escape the highly sticky substance. This phenomenon is frequently observed on species of *Cavendishia* which secrete a viscid latex (e.g., *C. lactiviscida, C. ciliata, C. panamensis,* etc.).

Cavendishia chiriquiensis var. **bullata** Luteyn, var. nov.

A var. *chiriquiensi* foliis valde bullatis, rhachidibus longioribus, bracteolarum et hypanthii forma, corollarum pubescentia, et distributione geographica differt.

TYPE. PANAMA. COCLÉ: 7 km N of El Copé, near Rivera Sawmill, 70–850 m, 10 Sep. 1977, *Folsom 5239* (MO, holotype).

Other Specimens Examined: PANAMA. CHIRIQUÍ: Cerro Colorado, road along top, 1500–1750 m, *Folsom et al. 4694* (MO). Cerro Colorado, cloud forest on continental divide, 1200–1500 m, *Mori & Dressler 7786* (MO, NY). 28 km from Río San Félix bridge, 1500 m, *Sullivan 280* (DUKE, MO).

Cavendishia chiriquiensis A. C. Smith has been collected from three geographically and altitudinally separated areas—the Boquete region at 1,700–1,900 m (type location of var. *chiriquiensis*), the Cerro Colorado area at 1,200–1,750 m, and now the region of El Copé at 700–850 m.

Cavendishia chiriquiensis var. *bullata* is restricted to Cerro Colorado and El Copé and differs from the typical variety primarily in the characters mentioned in the diagnosis and in several supporting character-features noted in Table 1. The Cerro Colorado populations themselves are somewhat intermediate in leaf size, shape and venation, in rachis length, in floral bract length, in calyx lobes, and in corolla pubescence. However, the overriding characters of bullate leaves and the usually longer rachises give it and the El Copé population a very different appearance, and one which merits varietal recognition.

One collection of var. *bullata* from Cerro Colorado, *Mori & Dressler 7786*, was annotated as *C. chiriquiensis* in 1976 and was so cited in the treatment for the *Flora of Panama* (Wilbur & Luteyn, 1978). Many more collections of both varieties are needed from areas between Boquete, Cerro Colorado and El Copé to understand the variation which is only now coming to light.

Cavendishia fortunensis Luteyn, sp. nov.

Frutex epiphyticus. Folia elliptica, (5–)7–11 cm longa, 2–4 cm lata; petioli 3–5 mm longi. Inflorescentia racemosa, floribus 20; rhachides 11 cm longae; bracteae florales oblongae vel ovalo-ellipticae, 21–23 mm longae, marginibus glandulosae; pedicelli 5–7 mm longi; bracteolae oblongo-oblanceolatae, 12–14 mm longae, marginibus glandulosae. Calyx glaber, hypanthio dense glanduloso; limbus campanulatus, lobis calloso-incrassatis. Corolla 19 mm longa. Stamina 17 mm longa, filamentis alternatim 2.5 mm et 6 mm longis, antheris tubulis inclusis alternatim 13 mm et 16.5 mm longis, poris 5–6 mm longis.

Epiphytic *shrub*; branches subterete or bluntly angled, slightly striate, glabrous, with scattered globular glands, reddish brown when dry. *Leaves* elliptic, (5–)7–11 cm long, 2–4 cm broad, basally obtuse or narrowly rounded, apically acuminate, sometimes abruptly short caudate-acuminate, reddish brown when dry, glabrous but with scattered, elevated, black globular glands 0.1 mm in diameter along the upper leaf surface, these often caducous leaving a reddish

TABLE 1. Comparison of *Cavendishia chiriquiensis* var. *chiriquiensis* and var. *bullata*.

	Var. *chiriquiensis*	Var. *bullata*	
	Boquete	Cerro Colorado	El Copé
Leaves	ovate; caudate-acuminate; 4.5–8 cm long; 3–5-plinerved, flat, not bullate	elliptic; caudate-acuminate; 4.5–6 cm long; 3–5-plinerved, 3 nerves usually impressed	lanceolate; caudate-acuminate; 7–9 cm long; 5-plinerved, 5 nerves deeply impressed
Inflorescence	6–9(–11)-flowered	(7–)10–12-flowered	9–11-flowered; but the lowest 2 nodes often sterile
Rachis	1.5–4.5 cm long; globular glands rare; sometimes flexuous	(2.5–)6–7.5 cm long; globular glands often dense in the basal 1 cm; nonflexuous	10.5 cm long; globular glands over the entire length; nonflexuous
Floral bracts (length)	15–25 mm	17–20 mm	20–26 mm
Bracteoles	linear to linear-lanceolate	oblong-ovate	ovate to oblong-ovate
Hypanthium	slightly apophysate	apophysate	apophysate
Calyx lobes	apiculate; entirely to nearly entirely callose thickened	0.5–0.75 mm; almost entirely callose thickened	1.5 mm; marginally callose thickened
Corolla	pilose distal in the ⅓	glabrous, rarely weakly puberulous in the distal ⅓	glabrous

"punctate" scar, 5(–7)-plinerved, the innermost lateral nerves arising slightly above the base, the midrib and lateral nerves deeply impressed above and conspicuously raised beneath causing the leaves to be bullate, the veinlets slightly impressed above and raised beneath; petioles subterete, rugose, 3–5 mm long, 2.5–3 mm in diameter, hirsute, with globular glands 0.2 mm in diameter in the distal portion. *Inflorescence* viscid, ca. 20-flowered, the lowest few nodes sterile; rachis subterete, bluntly angled, striate, glabrous, at least 11 cm long (the upper portion still in bud) and 3 mm in diameter at the base, with globular or angular glands ca. 0.2 mm long scattered along its length; floral bracts oblong to oval-elliptic, glabrous, rose, basally narrowed, truncate and clasping, apically rounded, 21–23 mm long, 10–11 mm broad, marginally crisped and with 12–20 dark red globular glands 0.1–0.2 mm in diameter on each side; pedicels subterete, swollen distally, striate, glabrous, 5–7 mm long, 0.75 mm in diameter, with globular glands concentrated at the distal swollen portion; bracteoles oblong-oblanceolate, 12–14 mm long, 6–8 mm broad, located midway along the pedicel and clasping or nearly concealing the entire calyx and lower $^1/_5$ of the corolla at anthesis, the margins cripsed and with dark red globular glands scattered along the edge. *Flowers* with the calyx glabrous, ca. 3.5–5 mm long, the hypanthium cylindric, obscurely ribbed, 1.5–2 mm long, basally truncate, covered by globular or angular glands 0.2 mm in diameter, the limb spreading-campanulate, 2–3 mm long including the lobes, both covered by globular glands, the lobes broadly triangular, 1 mm long,

completely glandular callose-thickened the distal ⅔, erect after anthesis, the sinuses flat to broadly rounded; corolla ca. 19 mm long, 4 mm in diameter, slightly narrowed distally, glabrous without but sparsely pilose within, pink, the lobes triangular, acute to obtuse, 1 mm long; stamens 17 mm long, the filaments distinct, alternately 2.5 mm and 6 mm long, the short filaments sparsely pilose dorsally at the distal tips, the long filaments densely pilose ventrally in the distal half, the anthers including the tubules alternately ca. 13 mm and 16.5 mm long, the thecae ca. 7 mm long, the dehiscence pores 5–6 mm long; style ca. 19 mm long, glabrous. *Berry* not seen.

TYPE: PANAMA. CHIRIQUÍ: E del sitio de presa en Fortuna, 6 Mayo 1976 *Mendoza 338* (DUKE, holotype; PMA, isotype, not seen; photo NY).

In the key to *Cavendishia* from Panama (Wilbur & Luteyn, 1978), this new species would key closest to *C. chiriquiensis* but would have some characters of *C. panamensis*. Upon closer examination, however, it is seen to be phenetically most similar to *C. pseudo-stenophylla*, differing most conspicuously in its elliptic (not linear-elliptic) leaves, glabrous bracts and corollas, and shorter bracteoles and corollas. These four species form a close and distinct group within the genus and are restricted to the mountains of Veraguas and Chiriquí provinces (see also Luteyn, 1976, for further discussion of this group).

Cavendishia quereme (H.B.K.) Bentham & Hooker

This species, recently collected in Panama, was known previously only from the Central Valley of Costa Rica and the region of Queremal in western Colombia. The Panamanian collections are morphologically similar to the specimens from Costa Rica and Colombia.

Specimens Examined: PANAMA. CHIRIQUÍ: Camino a Soledad, SO del campamento Fortuna (sitio de presa) desde la region de la finca Pitti, *Correa et al. 2211* (MO). Camino hacia la finca Landau, NE del campamento de Fortuna (Hornito), sitio de presa, 1100 m, *Correa et al. 2365* (DUKE). Al este del sitio de presa en Fortuna, *Mendoza et al. 112* (DUKE).

Didonica panamensis Luteyn & Wilbur, sp. nov.

Frutex epiphyticus. Folia elliptica vel ovato-lanceolata, 4–7 cm longa, (1.5–)2–3.5(–5) cm lata, basi attenuato, apice acuminata. Inflorescentia axillaris, racemosa, floribus 3–4(–5); pedicelli 15–25 mm longi. Hypanthium ad pedicellum articulatum, 3–4 mm longum; limbus calycis 7–9 mm longus lobis inclusis; lobi apiculati, 1 mm longi. Corolla campanulato-cylindrica, 12–13 mm longa. Stamina 10, 12–14 mm longa; filamenta 4–5 mm longa; antherae 10–12 mm longae tubulis inclusis; tubuli 4.5–5.5 mm longi. Stylus 18–19 mm longus.

Epiphytic *shrub*, glabrous except for the filaments; mature stems terete or subterete, grayish brown, the bark adherent or exfoliating in thin longitudinal strips, the immature stems bluntly angled, reddish. *Leaves* elliptic to ovate-lanceolate, 4–7 cm long and (1.5–)2–3.5(–5) cm broad, basally slightly tapering and attenuate, apically acuminate, sometimes abruptly so, the margins obscurely and remotely crenate, each crenation tipped by a tiny reddish brown gland, abundantly provided beneath with minute glandular fimbriae arising from concave depressions in the leaf surface, 3(5)-plinerved, the midrib conspicuously impressed above, elevated beneath, the lateral nerves arising slightly above the base and slightly elevated on both surfaces; pseudostipules ca. 1.5 mm long; petiole subterete, rugose, 6–12(–15) mm long, 2–3 mm wide, flanked the entire length by

the attenuate leaf blade. *Inflorescence* axillary, racemose, 3–4(–5)-flowered; rachis subterete, striate, 3–6 mm long and 2 mm broad at anthesis but extending to 13 mm; floral bracts ovate, acuminate, 1.5 mm long, 1.5 mm broad, marginally glandular-fimbriate; pedicels terete, striate, 15–25 mm long, ca. 1 mm in diameter, expanding to 2 mm in diameter at the distal tip, articulate with the hypanthium; bracteoles ovate, sharply acuminate to awl shaped, ca. 1 mm long, ca. 1 mm broad, located ⅓ of the way up the pedicel, marginally glandular-fimbriate. *Flowers* with the calyx 11–12 mm long, the hypanthium subcylindric or slightly spreading, slightly rugose, 3–4 mm long, ca. 4 mm in diameter, the limb spreading, somewhat campanulate, slightly rugose, 7–9 mm long including the lobes, 11–13 mm in diameter at the distal tip, the lobes barely differentiated, broadly ovate, apiculate, ca. 1 mm long, 6 mm broad at the base; corolla broadly campanulate-cylindric, 12–13 mm long, 12–13 mm broad, pale yellowish green, surface of the lower half drying smooth, the upper half slightly papillate, the lobes triangular, 3–4 mm long, 4–5 mm broad, erect; stamens 10, equal, 12–14 mm long, the filaments distinct, 4–5 mm long, marginally and dorsally long pilose and with glandular-fimbriate trichomes dorsally along the upper half of the filament and connective, the anthers including the tubules 10–12 mm long, slightly incurved at the base, the thecae minutely granular, 5.5–6.5 mm long, the tubules rigid, spreading, 4.5–5.5 mm long, dehiscing latrorsely by ovate-elliptic clefts 2–3 mm long, the inner surface moderately provided with apicular trichomes to 1 mm long; style glabrous, 18–19 mm long, exserted. *Berry* not seen.

TYPE: PANAMA. COCLÉ: Continental divide N of Penonomé on road to Coclesito between Llano Grande and Cascajal, in forest remnant, 1600 ft, 2 May 1979, *Hammel 7223* (MO, holotype).

Other Specimen Examined: PANAMA. COCLÉ: Continental divide ridge, Coclesito Road, *Hammel 2537* (MO).

Didonica panamensis is the second species in this recently described genus (Luteyn & Wilbur, 1977). Its stamens agree exactly with those of *D. pendula* Luteyn & Wilbur, the type of the genus, providing further support for this generic distinction. The new species differs significantly, however, from *D. pendula* in characters which modify the generic description: (1) the inflorescences of *D. panamensis* are racemose, being composed of 3–5 flowers, not of solitary flowers as *D. pendula*; (2) the pedicel and calyx of *D. panamensis* are articulate, not continuous as in *D. pendula*. Other specific differences are the shorter pedicels of *D. panamensis* (15–25 mm vs. 15–18 cm for *D. pendula*), and the glandular trichomes on the filaments and connectives of *D. panamensis*. The discovery of this new species has not, unfortunately, given us any new insight into the evolutionary relationships of *Didonica* with any other vaccinoid genus.

Disterigma hammelii Wilbur & Luteyn, sp. nov.

Frutex epiphyticus; ramulis pilosulis. Petioli 0.5–1 mm longi, glabri; lamina coriacea, glabra integra, elliptica vel lance-elliptica, (4–)5–7(–8) mm longa, 1.5–2.2(–3.0) mm lata. Hypanthium glabrum, 1.5–1.8 mm longum, 1.0–1.4 mm diametro; lobi calycis 4, erecti, acuti, lanceolati, 2.5–3 mm longi, ciliati. Corolla subrosa; tubus cylindraceus, 10–12 mm longus, 2.5–3.2 mm diametro; lobi 4, reflexi, 2.2–3 mm longi, lanceolati, pubescenti. Stamina 8; filamenta 8–9 mm longa, antherae lanceolatae, papillatae 1.2–1.5 mm longae, tubuli antherarum 2, 2.5–2.8 mm longi.

Straggly epiphytic *shrub*; branchlets irregularly ridged and grooved, the recent growth reddish brown and densely spreading pilosulose with tawny to reddish brown trichomes 0.4–1.0 mm long, the older growth dull brownish to grayish and only moderately pilosulose with hyaline to tawny trichomes; internodes short, almost all less than ¼ the length of the subtending leaves and usually 1–2 mm long. *Leaves* coriaceous, entire, elliptic to lance-elliptic, (4.0–)5–7(–8) mm long, 1.5–2.2(–3.0) mm wide, mostly about 2.5 times as long as wide, apically acute in general outline but the actual apex obtuse, gradually tapering basally into the petiole, glabrate on both surfaces and margins, rarely with a few appressed, reddish glandular trichomes on the lower surface, the midvein slightly elevated beneath but the venation otherwise indistinct, apparently dark green above and pale green beneath; petioles 0.5–1 mm long, glabrous or nearly so. *Inflorescence* of solitary flowers in the axils of foliage leaves, subtended by several (5–8) ovate to broadly elliptical, tawny to dull reddish brown, scarious bracts mostly to 0.8–1.2 mm long; bracteoles 2, broadly clasping, ovate to broadly oblong, broadly rounded apically, scarious, pale greenish to yellowish, striate, 2–2.7 mm long, borne just beneath and embracing the hypanthium; pedicels ca. 0.5 mm long and obscured from view by the bracts and bracteoles. *Flowers* with the hypanthium terete, campanulate to obconic, glabrous to sparingly pilosulose, pale greenish, 1.5–1.8 mm long, 1.0–1.4 mm in diameter, the calyx lobes 4, strongly ascendent, narrowly lanceolate, acute, with incurved margins, 2.5–3 mm long, entire, ciliate for the distal ⅓–½ but otherwise glabrous; corolla "pale pink," the tube cylindric, 10–12 mm long, 2.5–3.2 mm in diameter, nearly glabrous but usually with a few appressed glandular trichomes ca. 0.1 mm long just above the middle, the lobes 4, ascendent to more typically reflexed at maturity, 2.2–3 mm long, lanceolate, acute, distally spreading short-pubescent with hyaline trichomes; stamens 8, about as long or slightly longer than the corolla tube, the filaments 8–9 mm long, flattened, sparingly hyaline pilosulose with trichomes 0.2–0.6 mm long, the anthers lanceolate, the thecae minutely papillate 1.2–1.5 mm long, each tapering into a separate, slender tubule 2.5–2.8 mm long; style glabrous, exserted beyond the corolla tube, 13–14 mm long. *Berry* not seen.

TYPE: PANAMA. CHIRIQUÍ-BOCAS DEL TORO: Border trail along continental divide, ca. 5 mi NE of Boquete near Cerro Pate Macho above Palo Alto, 7100 ft, 23 May 1979, *Hammel 7390* (DUKE, holotype).

This species is named in honor of Mr. Barry Hammel who spent approximately 18 months collecting for the Missouri Botanical Garden in Panama. We are most appreciative of his special attention to the ericads during his botanical explorations.

Disterigma hammelii belongs to a small group of disterigmas which normally have a scandent, "wiry" epiphytic habit, short internodes, and narrowly lanceolate to nearly linear leaves less than 5 mm wide. This group ranges from western Panama to central Peru and includes *D. agathosmoides* (Weddell) Niedenzu, *D. weberbaueri* Hoerold, *D. panamensis* Standley, *D. luteynii* Wilbur, and *D. hammelii*. From this group the new species may be distinguished by its longer corolla and filaments, and by its exserted style.

The description of this species of *Disterigma* dramatically illustrates the impact of recent field work in Central America. A synopsis of the Central American

species was published seven years ago (Wilbur, 1974) summarizing all that was known of the genus in Central America at that time (three species, including one therein described as new). This is the third new species described since then and the sixth species that we recognize from Central America. We have seen a small, incomplete specimen from the "summit of Cerro Arizona, north of Santa Fé, Veraguas" (*Hammel 4742*, MO) which is undescribed. It has a 4-parted calyx and elliptic leaves about 20 mm long and half as wide lacking an apiculus. We await fuller material before formally describing it. A key distinguishing the six Central American species follows.

Key to the Central American Species of *Disterigma*

1. Lobes of the calyx and corolla 3; corolla deep red .... *D. trimerum* Wilbur & Luteyn
1'. Lobes of the calyx and corolla 4; corolla white or pale greenish.
  2. Thecae of anthers both emptying into a single tubule 1.5 mm long; leaves mostly more than 1 cm long and wide, with an apicule 1–2 mm long .. *D. utleyorum* Wilbur & Luteyn
  2'. Thecae of anthers each emptying into its own tubule 2 mm long or longer; leaves mostly 1 cm or less long and wide, nonapiculate.
    3. Leaf blades 4 mm wide or wider; calyx lobes eciliate; calyx tube 4-angled in cross-section; Guatemala, Costa Rica, Panama (Chiriquí) and northern South America .... *D. humboldtii* (Klotzsch) Niedenzu
    3'. Leaf blades 1.5–4.5 mm wide; calyx lobes ciliate; calyx tube terete or nearly so in cross-section; endemic to Panama.
      4. Calyx lobes 2.5 mm long or longer; corolla tube 10 mm long or longer; corolla lobes 2.2 long or longer; filaments more than 7 mm long; Chiriquí-Bocas del Toro, Panama .... *D. hammelii* Wilbur & Luteyn
      4'. Calyx lobes 2.5 mm long or less; corolla tube 6 mm long or less; corolla lobes less than 2 mm long; filaments less than 6 mm long; Panamá and Darién, Panama.
        5. Calyx lobes 2–2.5 mm long; leaves typically widest at or near the middle, usually linear, mostly ca. 4 times as long as wide; Darién .... *D. panamense* Standley
        5'. Calyx lobes 1.5–1.7 mm long; leaves typically widest decidedly above the middle, oblanceolate, mostly ca. 3 times as long as wide; Panamá .... *D. luteynii* Wilbur

Lateropora tubulifera Wilbur & Luteyn, sp. nov.

Frutex ca. 1.5 m altus. Folia coriacea, elliptica, 2.5–3.8 cm longa, 1.2–1.8 cm lata; petioli glabri, 3–4 mm longi. Inflorescentia axillaris, corymboso-racemosa, 2–3 cm longa; bracteae ovatae vel oblongae, 1.5–2.5 mm longae, 1.5–2 mm latae, ciliatae; pedicelli 10–18 mm longi, glabri; bracteoli ciliati, 2–2.2 mm longi, 1.5–1.8 mm lati, ciliati. Hypanthium ad pedicellum articulatum, campanulatum, 5-angulatum, 3–3.5 mm longum, glabrum; lobi calycis 5, erecti, triangulares, acuti, glabri, 1.0–1.5 mm longi. Corolla urceolata, 3.5–5 mm longa, extus glabra, intus villosa; lobi corallae 5, triangulares, acuti, 1–1.2 mm longi, intus villosi. Stamina 10; filamenta 2–2.2 mm longa, supra pilosa; thecae granulosae, ca. 2.5–3.0 mm longae; tubuli ca. 0.8 mm longi.

Shrub 1.5 m tall; immature branchlets moderately thick, 2–2.5 mm in diameter, glabrous, dark purplish, striate to irregularly angulate, the mature branches grayish to brownish. *Leaves* coriaceous, elliptic, 2.5–3.8 cm long, 1.2–1.8 cm wide, apically acute to obtuse and acutely tapering to the base, entire with an elevated or slightly thickened margin, glabrous or glabrate beneath, indistinctly pinnately veined; petioles glabrous, 3–4 mm long, 2–2.5 mm wide, flattened. *Inflorescence* axillary, corymbosely racemose, (1–)3–5-flowered, 2–3 cm long; rachis 1–1.5 cm long, glabrous; bracts 3–4, broadly oblong to orbicular, basal, peduncular, short-ciliate, 1–3 mm long, ca. 1.5–2.2 mm wide; floral bracts ovate to oblong, 1.5–2.5 mm long, 1.5–2 mm wide, glabrous except for short cilia, slightly keeled and

short-apiculate, irregularly narrowly hyaline margined; pedicels slightly clavate, 10–18 mm long, medially ca. 1 mm in diameter, glabrous except for an inconspicuous fringe of glandular trichomes 0.2–0.4 mm long borne distally just beneath the sharply delimited disarticulation groove; bracteoles subopposite to alternate, ovate to oblong, 2–2.2 mm long, 1.5–1.8 mm wide, ciliate, irregularly hyaline margined, appressed, located in the lower proximal third. *Flowers* with the hypanthium campanulate, clearly 5-angulate in the lower half with 5 rounded ridges ascending between the calyx lobes, 3–3.5 mm long, 3–3.2 mm in diameter at anthesis, glabrous, disarticulating from the pedicel by a clearly marked groove, the calyx limb somewhat flaring or at least wider than the hypanthium, glabrous, 0.7–1.0 mm long, the calyx lobes 5, erect, deltoid, acute, 1.0–1.5 mm long, basally 1.8–2.2 mm wide, glabrous; corolla urceolate, 3.5–5 mm long, "pink," externally glabrous, internally densely pilose to tangled villous in the distal half with white trichomes 0.6–1.0 mm long; corolla lobes 5, triangular, acute, 1–1.2 mm long, glabrous externally and densely tangled villous internally; stamens 10, the filaments flattened, 2.0–2.2 mm long, basally less than 0.5 mm wide, distally attached for about ⅓ the length from just above the strongly incurved base to the thecae, densely pilose distally with white trichomes 0.5–1.2 mm long, the anthers conspicuously granular, 2.5–3 mm long including the strongly incurved base of ¼–⅓ the length of the thecae but excluding the smooth, ca. 0.8 mm long tubules, dehiscing by a slit extending from the apex of the tubule to the pronounced basal curve.

TYPE: PANAMA. CHIRIQUÍ: Cerro Hornito, in cloud forest, 6000 ft, 8 May 1978, *Hammel 3069* (MO, holotype).

The specific epithet of this species refers to the tubules of the anthers which are at least twice as long as those of the other two known species. The leaf blades are less than 4 cm long and their smallness is in great contrast to the leaf blades of the other two species of this endemic Panamanian genus. A key to the genus follows.

Key to the Genus *Lateropora*

1. Calyx lobes 2–3 mm long, 4–5 mm wide basally; corolla lobes ca. 3 mm long; petioles 5–15 mm long; leaves 6–13 cm long, 4–9 cm wide .... *L. ovata* A. C. Smith

1'. Calyx lobes 2 mm long or less, 2.2 mm wide or less basally; corolla lobes less than 2 mm long; petioles 5 mm long or less; leaves 2.5–8.5 cm long, 1.2–4.5 cm wide.

   2. Leaves when young appressed strigillose beneath with trichomes 0.2–0.3 mm long; tubules of the anthers 0.3 mm long or less; leaf blades 3–8.5 cm long; Veraguas .... *L. santafeensis* Wilbur & Luteyn

   2'. Leaves glabrous beneath; tubules of the anthers ca. 0.8 mm long; leaf blades 2.5–3.8 cm long; Chiriquí .... *L. tubulifera* Wilbur & Luteyn

Macleania megabracteolata Wilbur & Luteyn, sp. nov.

Frutex epiphyticus. Lamina foliorum coriacea, elliptica, (5–)7–10(–12.5) cm longa, (2.7–)3–4.5 (–5.7) cm lata, apice acuta vel acuminata, basi cuneata vel rotunda, 5–7-plinervia. Inflorescentia axillaris, racemosa, 4–7 cm longa, floribus 4–7; bracteae oblongae vel spatulatae, 9–13 mm longae, integrae, ciliatae; bracteolae 2, ellipticae, acutae, 13–16 mm longae, ca. 5 mm latae; pedicelli articulati, 5–11 mm longi. Hypanthium angulatum, 5–7 mm altum; limbus calycis ca. 2 mm altus; lobi calycis 5, 3.5–4 mm longi, acuti, glanduloso-puberuli. Corolla 12–14 mm longa, glanduloso-puberula; tubus cylindricus, roseatus, 10–12 mm longus, 4.5–5 mm diametro; lobi 5, acuti, 2–2.5 mm longi. Stamina 10; filamenta distincta, 3–3.5 mm longa; thecae granulosae, ca. 3 mm longae; tubuli 2, 5–6 mm longi; pori obliqui introrsi, 0.6 mm longi.

Epiphytic *shrub*; stems strongly and coarsely ridged and grooved, glabrous or nearly so, brownish. *Leaves* coriaceous, elliptic, (5–)7–10(–12.5) cm long, (2.7–)3–4(–5.7) cm wide, basally rounded or broadly tapering, apically acuminate with the tip 1 cm or more long or acute, entire and slightly revolute, glabrous above or sparingly to moderately spreading short-pubescent or puberulent on the very base of the midvein, glabrate beneath with punctate depressions marking former trichome attachments or, especially in younger leaves, with minute, reddish brown appressed glandular trichomes 0.1–0.2 mm long, 5–7-plinerved, the secondary veins arising at or near the base with the midvein proximally prominently elevated and impressed distally while elevated beneath; petioles stout, rugose, 3–6 mm long, puberulous to glabrate. *Inflorescence* axillary, borne near the end of the branches, racemose, 4–7-flowered, the rachis, pedicels, bracts, calyces and corollas moderately provided with reddish brown appressed glandular trichomes 0.1–0.2 mm long; rachis striate or irregularly angled, 3–7 cm long, the lower 1.5–2 cm enveloped by ovate to oblong bracts 5–8 mm long; pedicels striate, 5–11 mm long, markedly broadened and articulate just beneath the hypanthium; floral bracts oblong to spatulate, 9–13 mm long, entire, apically rounded; bracteoles 2, borne just beneath the hypanthium, elliptic, acute, 13–16 mm long, ca. 5 mm wide. *Flowers* with the hypanthium basally strongly angulate or pentagonal from the prominently intersinal ridges in the lower half, 5–7 mm long, the calyx limb ca. 2 mm long, the 5 triangular deltoid calyx lobes 3.5–4 mm long, basally 3.2–4 mm wide, apically acute; corolla 12–14 mm long, the tube broadly cylindric, roseate, 10–12 mm long, 4.5–5.5 mm in diameter, the lobes triangular-deltoid, acute, 2–2.5 mm long, reportedly pale greenish; stamens 10, the filaments distinct, 3–3.5 mm long, spreading short-pubescent with slender trichomes 0.2–0.4 mm long, the anthers coarsely granular, ca. 3 mm long, each with two completely separate cylindrical tubules 5–6 mm long opening by an apical, introrse oval cleft; style glabrous, the stigma punctiform. *Fruit* unknown.

TYPE: PANAMA. CHIRIQUÍ: E de la presa en Fortuna, 22 Feb. 1976, *Mendoza, Mendieta & Mayo 191* (DUKE, holotype; PMA, isotype, 2 isotypes to be distributed).

This is the third known species of *Macleania* found north of South America in which each anther sac terminates in a distinct tubule. The bracteoles of the two previously known species, *M. rupestris* (H.B.K.) A. C. Smith [including *M. glabra* (Klotzsch) Hoerold] and *M. talamancensis* Wilbur & Luteyn, are less than 4 mm long while those of *M. megabracteolata* are longer than 12 mm.

Themistoclesia revoluta Wilbur & Luteyn, sp. nov.

Frutex epiphyticus. Lamina foliorum pinnatinervia, elliptica vel oblanceolata, 5–6.5(–7.5) cm longa, 9–14 mm lata, basi cuneata, apice obtusa vel rotundata, integra, revoluta, supra et subtus pubescentia; petioli 3–4 mm longi, puberuli. Racemi axillares, 5–10 cm longi; bracteae 2.5–4 mm longae; pedicelli 0.9–1.6 cm longi; bracteoli appressi, 2–3 mm longi. Hypanthium ad pedicellum non articulatum, 5-angulatum, pubescens; limbus calycis 1–1.2 mm longus, lobi ca. 1 mm longi. Corolla 5-angulata, 8–9 mm longa; tubus glabrus, 5–5.5 mm longus; lobi erecti, 2.5–3 mm longi, ciliati. Stamina 10, 6–8 mm longa; filamenta ciliata, 1.5–2 mm longa; antherae 2.5–3 mm longae; tubuli antherarum 2, distincti, 5–6 mm longi. Stylus 8–9 mm longus, glabrus.

Epiphytic *shrubs*; stems ridged and grooved but becoming terete, light brown to dun colored, minutely puberulent or short-pubescent. *Leaves* spirally ar-

ranged, narrowly elliptic to oblanceolate, 5–6.5(–7.5) cm long, 9–14 mm wide, basally cuneate, apically obtuse to rounded, entire, strongly revolute, moderately to densely short-pubescent on both the upper and lower surfaces, sparingly to moderately beset with glandular, reddish brown, appressed trichomes 0.1–0.2 mm long, the venation pinnate, the midvein prominently impressed above and elevated beneath, the secondary and tertiary veins when dry elevated above and moderately so beneath; petiole dorsally compressed and grooved, 3–4 mm long, inconspicuously puberulous to short-pubescent. *Inflorescence* borne at distal tip of the branches, axillary, racemose, 10–16-flowered; bracts 6–8, basal, appressed, lanceolate to narrowly triangular, acute, 3.5–5 mm long, finely short-pubescent abaxially; rachis ridged or striate, 5–10 cm long, densely short-pubescent with hyaline trichomes 0.2–0.5 mm long; floral bracts 2.5–4 mm long, narrowly triangular to narrowly lanceolate; pedicels 0.9–1.6 cm long, nonarticulate with the hypanthium, sharply striate, moderately to densely spreading short-pubescent with the slender, hyaline trichomes 0.2–0.3 mm long; bracteoles appressed, narrowly triangular, acute, spreading short-pubescent, keeled, 2–3 mm long, usually medial or submedial, alternate. *Flowers* with the hypanthium obpyramidal, strongly 5-angulate or winged, the wings alternate with the lobes, moderately spreading short-pubescent throughout, ca. 5 mm long, ca. 5 mm in diameter at the apex, the calyx limb 1–1.2 mm long, the calyx lobes depressed-triangular, acute to apiculate, ca. 1 mm long; corolla pentagonal, narrowly 5-winged opposite the lobes, 8–9 mm long overall, the tube tapering from the base to the apex, glabrous, 5–5.5 mm long, the lobes erect, 2.5–3 mm long, sparingly ciliate along the midrib, strongly reflexed at anthesis exposing the stamens and style; stamens 10, 6–8 mm long, alternately slightly unequal, the filaments equal, 1.5–2 mm long, sparsely ciliate and glandular-fimbriate, the anther thecae 2.5–3 mm long, basally tapering into a short-setose appendix, closely coherent basally due to the interlocking of the antheridial grooves; tubules 2 per anther, separate, twice as long as the thecae or 5–6 mm long, tapering upward and opening by a slender introrse slit ca. 1.5 mm long; style 8–9 mm long, glabrous, the stigma punctiform. *Fruit* unknown.

TYPE: PANAMA. CHIRIQUÍ; Bajo-Fortuna, 19 Mar. 1976, *Mendoza, Mendieta & Mayo 258* (DUKE, holotype; PMA, isotype).

Additional Specimen Examined: PANAMA. CHIRIQUÍ: Desembocadura del Río Hornitos, *Mendoza et al. 239* (PMA).

This species is unlike any other Central American species of *Themistoclesia* in its narrow, strongly revolute leaves and long-pedicelled flowers borne in elongate racemes. It is most closely related to *T. cutucuensis* A. C. Smith from eastern Ecuador and adjacent Peru, but differs in its densely scabrous inflorescences (including rachises, pedicels, bracts and calyces); its strongly revolute leaves with longer petioles, pinnate venation, and tapering (not subcordate) bases; and in its glandular anther connectives. A key to the Central American species of *Themistoclesia* follows.

Key to the Central American Species of *Themistoclesia*

1. Staminal tubules 1 per anther with a single introrse cleft; hypanthium distinctly 5-winged; leaves apically obtuse .... *T. pentandra* Sleumer

1'. Staminal tubules 2 per anther, the tubules either separate or united but with 2 introrse clefts; hypanthium bluntly 5-angled, not winged; leaves apically acute or acuminate.
  2. Corolla 2.5–3.5 mm long; leaves less than 1.9 cm long, cuneate .... *T. smithiana* (Standley) Sleumer
  2'. Corolla 5–9 mm long; leaves more than 2 cm long.
    3. Corolla narrowly 5-winged, 8–9 mm long; leaves 5–7 cm long, strongly revolute; flowers in 10–16-flowered racemes .... *T. revoluta* Wilbur & Luteyn
    3'. Corolla not winged, 5–6 mm long; leaves 2–2.5 cm long, not at all revolute; flowers solitary.
      4. Bracteoles ovate to hemispheric, completely concealing the glabrous pedicel; corolla cylindric, pilosulose throughout; stamens 5 mm long, the filaments pilosulose, the anther basally minutely appendiculate .... *T. costaricensis* Luteyn & Wilbur
      4'. Bracteoles awl shaped, never concealing the pilosulose pedicel; corolla urceolate, pilosulose distally; stamens 2.5 mm long, the filaments glabrous, the anther without a basal appendage .... *T. horquetensis* Luteyn & Wilbur

Vaccinium dissimile Blake

This peculiar creeping vine is easily overlooked and, at the time the account of the Ericaceae was prepared for the *Flora of Panama*, it was unknown from the Province of Colón.

Specimen Examined: PANAMA. COLÓN: S approach of Cerro Bruja from Río Escandaloso, *Hammel 3123* (MO).

Vaccinium jefense Luteyn & Wilbur

When described, this species was thought to be a narrow endemic in the vicinity of Cerro Jefe, an approximately 1,000 meter elevation mountainous area just east of the Canal Zone. It is now known from several collections made along the Continental Divide in Coclé Province.

Specimens Examined: PANAMA. COCLÉ: Summit of Alto Calvario, 900 m, *Folsom & Robinson 2402* (MO); *Folsom 2685* (MO). 7 km N of Llano Grande on road to Coclesito, 1700 ft, *Hammel 1942* (MO). Near Sawmill above El Copé, 3000 ft, *Hammel 2363* (MO).

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ADDITIONAL PANAMANIAN SPECIES OF *BURMEISTERA* (CAMPANULACEAE: LOBELIOIDEAE)[1]

ROBERT L. WILBUR[2]

ABSTRACT

Burmeistera hammelii Wilbur and *B. mcvaughii* Wilbur are newly described from Panama. *Burmeistera obtusifolia*, previously known only from Costa Rica, is recorded for the first time from Panama. A key to all Panamanian species of *Burmeistera* is included.

Barry Hammel spent approximately eighteen months as the Missouri Botanical Garden's collector in Panama. He proved himself to be a very zealous collector and his particular attention to the genus *Burmeistera*, for which I am most appreciative, resulted in the following additions to the known lobeliad flora of Panama. Since the two previously undescribed species of *Burmeistera* and the range extension of a Costa Rican species into Panama are a significant increase in the number of species known from Panama, it seems desirable to include a new key to facilitate their determinations. Species numbered 1–16 are described in Wilbur (1976) while X1–X3 are discussed after the present key.

1. Median cauline leaves more than 8 times as long as wide, narrowly linear .... 1. *B. chiriquiensis* Wilbur
1′. Median cauline leaves less than 6 times as long as wide, ovate, lanceolate, elliptic or at least not narrowly linear.
  2. Anthers externally pilose with golden trichomes; plants vegetatively entirely glabrous .... 8. *B. microphylla* Donnell Smith
  2′. Anthers either glabrous externally or with white or sordid, grayish trichomes; plants vegetatively either glabrous or pubescent.
    3. Flowers 2.9 cm long or less.
      4. Filament tube 10 mm long or more; hypanthium 3–6 mm long; corolla yellow or greenish.
        5. Corolla yellow; calyx lobes acute, deltoid; filament puberulous .... 11. *B. parviflora* F. E. Wimmer ex Standley
        5′. Corolla greenish; calyx lobes obtuse, oblong; filament tube distally glabrous .... 9. *B. morii* Wilbur
      4′. Filament tube less than 9 mm long; hypanthium ca. 3 mm long; corolla purplish .... 7. *B. kirkbridei* Wilbur
    3′. Flowers 3 cm long or longer.
      6. Hypanthium in anthesis cylindric to campanulate or urceolate, basally somewhat rounded and with the sides more or less parallel.
        7. Leaves lanceolate to lance-ovate, gradually long-acuminate from below the middle, 2.5 cm wide or less; plants vegetatively entirely glabrous .... 6. *B. glauca* (F. E. Wimmer) Gleason
        7′. Leaves elliptic, ovate or broadly lanceolate, usually wider than 2.5 cm; plants vegetatively usually somewhat puberulent or scaberulent.
          8. Calyx lobes 5 mm long or less.
            9. Leaf margins conspicuously denticulate or serrulate with (4–)5–9 teeth per cm .... X1. *B. hammelii* Wilbur
            9′. Leaf margins inconspicuously serrulate with 3 or fewer teeth per cm.
              10. Corolla puberulous; calyx lobes and hypanthium apiculate to puberulous; berry red .... 5. *B. dukei* Wilbur

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10'. Corolla glabrous; calyx lobes and hypanthium glabrous; berry white or greenish turning blackish.
11. Upper corolla lobes less than 12 mm long and the 2 lateral lobes about 7 mm long; corolla greenish; anthers externally puberulous ..... 12. *B. pirrensis* Wilbur
11'. Upper corolla lobes 18 mm long or longer and the 2 lateral lobes 12–14 mm long; corolla dark red; anthers externally glabrous ..... 3. *B. darienensis* Wilbur
8'. Calyx lobes usually more than 5 mm long.
12. Two lower anthers densely bearded apically with a dense tangle of trichomes; leaves mostly 5 cm or more wide; plants of Darién ..... 10. *B. panamensis* Wilbur
12'. Two lower anthers sparingly fringed apically or glabrous with not more than a sparse fringe of trichomes; leaves mostly less than 5 cm wide; plants from west of Darién.
13. Corolla green or bronzy; hypanthium and calyx lobes green, drying green or stramineous, rarely suffused with purple or maroon; berry greatly inflated with a thin, bladdery wall, 2–4 cm in diameter and 2.5–5 cm long ..... 16. *B. vulgaris* F. E. Wimmer
13'. Corolla predominantly purplish or green with a deep suffusion of maroon or dark purple; hypanthium and calyx lobes purplish and drying dark purplish or blackish; berry fleshy and with a substantial, thick wall, 1–2(–2.5) cm in diameter and 1–2(–3) cm long ..... 2. *B. cyclostigmata* Donnell Smith
6'. Hypanthium in anthesis obconic, acutely tapering at the base with the sides strongly divergent.
14. Leaf margins conspicuously denticulate or serrulate with 6 or more teeth per cm ..... X2. *B. mcvaughii* Wilbur
14'. Leaf margins entire to inconspicuously serrulate with 4 or fewer teeth per cm.
15. Calyx lobes 5 mm long or more.
16. Stems densely spreading hirsute with the trichomes visible without magnification; calyx lobes spreading or even reflexed, 5–10 mm long, 2.5 mm wide or wider ..... X3. *B. obtusifolia* F. E. Wimmer
16'. Stems glabrous or inconspicuously appressed pubescent; calyx lobes ascendent, (7–)11–20 mm long, 2 mm or less wide ..... 13. *B. tenuiflora* Donnell Smith
15'. Calyx lobes less than 4 mm long.
17. Corolla tube puberulent or inconspicuously appressed short-pubescent.
18. Pedicels and hypanthia glabrous to moderately spiculate or appressed short-pubescent or even strigillose; Panama east of Volcán Chiriquí ..... 4. *B. dendrophila* F. E. Wimmer
18'. Pedicels and hypanthia moderately to densely spreading short-pubescent; Panama west of Volcán Chiriquí ..... 15. *B. utleyi* Wilbur
17'. Corolla tube glabrous.
19. Filaments distally glabrous; anther tube externally glabrous; upper corolla lobes 7 mm long ..... 14. *B. toroensis* Wilbur
19'. Filaments distally puberulous; anther tube externally puberulous; upper corolla lobes 10 mm long or longer ..... 4. *B. dendrophila* F. E. Wimmer

X1. Burmeistra hammelii Wilbur. TYPE: Panama, Darién, NE slope of Cerro Sapo, approach from Garachiné, 3200 ft, *Hammel 7274* (DUKE, holotype; MO and 1 sheet to be distributed, isotypes).

Planta erecta vel scandenta, ca. 1 m alta; ramuli puberuli vel glabrati. Lamina foliorum ovata vel elliptica, 7–19 cm longa, 3.5–9 cm lata, ca. 2-plo longiora quam lata, acuta vel acuminata ad apicem et basi rotundata vel cuneata, margine serrulata 4–9 serrulatis per cm; venulosi infra strigillosi; petioli puberuli, 0.8–4 cm longi. Flores 3–4 cm longi; pedicelli glabri, 3–4 cm longi. Hypanthium cylindricum

vel obconicum, glabrum, 4–5 mm longum, 3–4 mm latum; lobi calycis deltoidi vel oblongi, acuti vel obtusi, denticulati, glabri, 2–3 mm longi. Corolla glabra, virenta; tubus 1.5–2 cm longus, ca. 2–3 mm diametro; lobi lineari vel oblongi, superiori 12–16(–18) mm longi, laterati 7–9 mm longi, inferiori 5–6.5 mm longi. Filamenta glabra vel puberula, 22–27 mm longa; tubus anthearum appressi-pilosus, 4–6 mm longus. Bacca globosa, 5–6 mm longa, 6–8 mm lata.

Erect to scandent *herb* to 1 m tall; branches inconspicuously puberulous to glabrate. Principal *leaves* with blades ovate to broadly elliptic, 7–19 cm long, 3.5–9 cm wide, ca. 2 times as long as wide, apically acute to more typically acuminate, basally rounded to somewhat cuneate, marginally conspicuously serrate throughout with ca. 4–6(–9) teeth/cm each ca. 1–1.5 mm long, glabrous on the upper surface and densely strigillose along the veins beneath; petioles 0.8–4 cm long, sparingly to moderately but always inconspicuously puberulous. *Flowers* 3–4 cm long at anthesis; pedicels solitary in the axils of the reduced (1.5–4 cm long) upper leaves and thus racemous, strongly ascendent to wide spreading, glabrous, 3–4 cm long, 1–2 mm in diameter, ebracteolate; hypanthium in anthesis cylindric to obconic, glabrous, basally acute to rounded, 4–5 mm long, 3–4 mm in diameter medially; calyx lobes deltoid to oblongish, acute to obtuse, denticulate, glabrous, 2–3 mm long, 1.5–2 mm wide basally; corolla glabrous, green, the tube 1.5–2 cm long, 2–3 mm in diameter, the lobes linear to narrowly oblong, the upper lobes falcate, 12–16(–18) mm long, the lateral lobes 7–9 mm long, the lowermost lobe 5–6.5 mm long; filament tube glabrous to puberulous, 22–27 mm long, the anthers externally appressed-pilosulose, 4–6 mm long, the lowest anthers slightly pilose-fringed. *Berries* globose, 5–6 mm long, 6–8 mm in diameter.

This species is known only from the type collection made on the Cerro Sapo in Darién. It is named for the collector, Barry Hammel, who through his particular attention to the genus *Burmeistera*, has considerably advanced our understanding of the Panamanian representatives.

X2. Burmeistera mcvaughii Wilbur. TYPE: Panama, Chiriquí-Bocas del Toro, border trail along continental divide ca. 5 mi NE of Boquete near Cerro Pate Macho above Palo Alto along trail above 6800 ft, *Hammel 7399* (DUKE, holotype; MO, plus 6 specimens to be distributed, isotypes).

Planta suffruticosa; ramuli puberuli. Lamina foliorum elliptica, 6–12(–16) cm longa, 3–5(–7) cm lata, 1.5–2(–3) plo longiora quam lata, acuta vel acuminata ad apicem et basi acuta vel rotunda, margine serrulata vel denticulata, 6–8 denticulatis per cm; petioli puberuli, 2–3 cm longi; folia juvenilia pinnatifida, 1–3 dissecta. Flores 3.2–4 cm longa; pedicelli puberuli, 4–7 cm longi. Hypanthium obconicum, puberulum, costatum, 5–7 mm longum, 3–5 mm latum; lobi calycis linear vel lanceolati, serrulati, puberuli, 6–8 mm longi, 1–1.2 mm lati. Corolla puberula, virenta; tubus 12–18 mm longus; lobi oblongi vel deltoidi, superiori 10–13 mm longi, laterali 6–7 mm longi, inferiori ca. 5–7 mm longi. Filamenta 22–27 mm longa, puberula; tubus anthearum puberuli. Bacca cylindrica, ca. 15 mm longa, 10–12 mm lata.

Terrestrial, scandent *shrublet* up to 2.5 m long; stems inconspicuously and minutely puberulous above with trichomes 0.1 mm long or less, glabrate below. Principal *leaves* elliptic, 6–12(–16) cm long, 3–5(–7) cm wide, mostly 1.5–2(–3) times as long as wide, apically acute to more typically acuminate, basally acute to rounded, marginally conspicuously serrulate or denticulate throughout with ca. 6–8 teeth/cm each ca. 0.2–0.4 mm long, inconspicuously and sparingly microscopically puberulous on the veins above or glabrate, moderately and incon-

spicuously microscopically puberulous on the veins beneath, the veins forming a conspicuous reticulum with a more or less distinct marginal vein ca. 1 mm from the edge; juvenile leaves greatly dissected, 1–2-pinnatifid; petioles mostly 2–3 cm long, sparingly puberulous to glabrate. *Flowers* 3.2–4 cm long; pedicels solitary in the upper leaf axils, ascendent, straight to somewhat curving, puberulous, ebracteolate, 4–7 cm long; hypanthium at anthesis obconic, basally acute, moderately to densely but microscopically puberulent, the trichomes less than 0.1 mm long, slightly curved and mostly restricted to the 10 proximal vertical costae, 5–7 mm long, distally 3–5 mm in diameter; calyx lobes linear to narrowly lanceolate, acute, inconspicuously serrulate, ascendent, inconspicuously minutely puberulous on both surfaces with hyaline trichomes 0.1 mm long, 6–8(–9) mm long, medially 1–1.2 mm wide; corolla moderately to densely but inconspicuously puberulous with hyaline trichomes 0.1 mm long or less, pale green, the tube 12–18 mm long, the lobes falcately oblong to deltoid, acute, the 2 upper lobes 10–13 mm long, the 2 lateral lobes 6–7 mm long, the lowermost lobe 5–7 mm long; filament tube exserted, 22–27 mm long, distally moderately spreading puberulous, the anthers 3–5 mm long, moderately to densely spreading puberulous, apically with the two shortest anthers with a short pilose fringe. *Berries* broadly cylindric, ca. 15 mm long, 10–12 mm in diameter.

This species seemingly most closely resembles *Burmeistera dendrophila* F. E. Wimmer and *B. utleyi* Wilbur which are also known only from the mountainous border area between the Panamanian provinces of Chiriquí and Bocas del Toro. *Burmeistera mcvaughii* differs from both of these species in its more broadly elliptical leaves and pronouncedly serrulate to denticulate margin and its narrowly lanceolate to linear, acute calyx lobes. Barry Hammel, who has had the most field experience with these species, has observed that *B. mcvaughii* occurs at somewhat higher elevations and in more exposed, mist-swept habitats.

The species is named, as a small token of esteem, for Professor Rogers McVaugh who has recently retired from his role as Professor of Botany and Curator of Vascular Plants at the University of Michigan. Among his numerous botanical achievements, he has long been the leading student of the American Campanulaceae; hence it is most fitting that his labors of more than forty years ago in producing the basic treatment of the lobeliads for the *North American Flora* be recalled by those of us who have been attracted to these plants not only by their beauty but by the availability of his eminently useful account. All wish him well in his efforts to complete the extremely ambitious *Flora Novogaliciana* upon which he has devoted so much effort during the past three decades. To complete it in a manner satisfying his own high standards will require a long, healthy and happy period of "retirement" and we all wish him that. The orthography of the specific epithet is not in accord with Recommendation 73C4 of the International Code; it is doubtful if Dr. McVaugh would approve such a rendition of his patronymie.

Other Specimens Examined: PANAMA. CHIRIQUÍ-BOCAS DEL TORO: In forest near top of continental divide ridge along trail towards Cerro Pate Macho, above Palo Alto, ca. 4 mi NE of Boquete, 6800 ft, *Hammel 6490* (DUKE, MO).

X3. Burmeistera obtusifolia F. E. Wimmer

This is the first collection of this species seen from Panama. Previously *Burmeistera obtusifolia* was known only from the northern slopes of the Cordillera de Talamanca in Costa Rica and apparently also from the Volcán Turrialba. The presence of this species in western Panama is a range extension of approximately 290 km and is another lobeliad now reported from western Panama, all of which were previously unknown from any area closer than the central Talamancas of Costa Rica. These recent extensions include, in addition to *B. obtusifolia*, *B. parviflora* F. E. Wimmer ex Standley, *Centropogon gutierrezii* (Planch. & Oerst.) F. E. Wimmer and *C. smithii* F. E. Wimmer. There are differences in both vegetative and floral pubescence and in floral dimensions between the Costa Rican and Panamanian collections but their importance can properly only be evaluated after additional collections have been made.

Specimens Examined: PANAMA. CHIRIQUÍ-BOCAS DEL TORO: Border trail along continental divide ca. 5 mi NE of Boquete near Cerro Pate Macho above Palo Alto, 7100 ft, *Hammel 7370* (DUKE, MO, and specimens to be distributed).

LITERATURE CITED

WILBUR, R. L. 1976. Campanulaceae. *In* R. E. Woodson, Jr. & R. W. Schery, Flora of Panama. Ann. Missouri Bot. Gard. 63: 593–655.

SAPOTACEAE OF PANAMA[1]

George E. Pilz[2]

Abstract

The *Flora of Panama* Sapotaceae treatment by Blackwell is updated. *Pouteria congestifolia* Pilz and *P. leptopedicellata* Pilz are newly described and the combination *Pouteria buenaventurensis* (Aubr.) Pilz is made. As now revised, the Panamanian flora includes 44 species in 11 genera, an increase from the 24 species in 6 genera known to Blackwell. This revision is based on collections made in the past decade.

Trees or shrubs with milky latex. *Leaves* alternate, rarely opposite; nodes mostly trilacunar, the traces evident on the leaf scar; blades simple, entire; pubescence of 2-armed hairs, one arm sometimes obsolete. *Flowers* solitary or clustered in axils or at recently defoliated nodes, rarely cauliflorous, perfect, rarely unisexual, actinomorphic; sepals in one or two whorls, rarely spiral, free or rarely united; corolla gamopetalous, the lobes simple or divided, usually as many as sepals; stamens generally as many as the corolla lobes and opposite them, the staminodes sometimes present between the corolla lobes, variously developed; pistil syncarpous, the style simple, sometimes obscurely lobed at the summit, the ovary superior, 1–14-loculed, the carpels uniovulate. *Fruit* a berry; exocarp usually fleshy, often becoming sclerotic; seeds 1–several, the testa hard, smooth, often shiny, the attachment area (scar) lateral or basal, variously developed, often rough and duller in color, the endosperm either copious on either side of the flat foliaceous cotyledons, or scanty, or absent with thick fleshy cotyledons.

Scarcely 12 years have elapsed since Blackwell (1968) published the treatment of Sapotaceae for the *Flora of Panama*. Blackwell treated 24 species in 6 genera, while the present study treats 44 species in 11 genera. Recent collections, particularly from moist forest areas, have significantly increased the number of taxa known from Panama, and they have also permited the first descriptions of flowers and/or fruits for several species. Still, all too many species have inadequate series of specimens, and collectors can greatly assist future monographers by seeking flowers and fruits of all but the most common cultivated species. Determination of geographical distribution and morphological variation of most species awaits further collection of specimens.

Collectors can also make valuable contributions by preserving viable seeds and/or developing flowers for cytological study. Sapotaceae are almost completely unknown cytologically, particularly American species. Patterns seen in a few chromosome counts that have been made of Old World taxa look interesting, and a more complete record might prove valuable in determining the natural affinities of certain species.

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Full descriptions are included in this treatment only for those taxa not treated by Blackwell (1968). Likewise, complete lists of synonyms are not included. The nomenclature used for American Sapotaceae has been in considerable flux, and it is by no means stabilized even now. Over 200 names have been proposed for the 44 species treated in this study. Nearly half of the later synonyms are nomenclatural, reflecting the widely different concept of genera held by various authorities. More complete lists of synonyms may be found in papers cited after the generic descriptions.

As a taxonomic result of this study I am describing two new species of *Pouteria* and transferring *Richardella buenaventurensis* to *Pouteria*.

Literature:

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a. Calyx biseriate, with two distinct series of 3/3 or 4/4 persistent sepals.
- b. Calyx of 3/3 sepals; fertile stamens 6; seed scar basilateral and several times longer than broad .... 5. *Manilkara*
- bb. Calyx of 4/4 sepals; fertile stamens 8; seed scar nearly basal and suborbicular .... 8. *Mimusops*

aa. Calyx with a single cycle or series of sepals, if distinctly biseriate then 2/2.
- c. Flowers with well-developed staminodes.
  - d. Seed scar small, basal or basilateral, never reaching the middle of the seed; stamens inserted at top of the throat in the sinuses between the corolla lobes; corolla lobes with lateral appendages or without appendages.
    - e. Corolla lobes with lateral appendages; petiole 0.2–2 cm long.
      - f. Seed with endosperm; plants unarmed; ovary usually glabrous; style 1.2–2 mm long; apex of the fruit tapering to a persistent style .... 3. *Dipholis*
      - ff. Seed without endosperm; plants often with spines; ovary usually pubescent; style 3–7 mm long; apex of the fruit rounded or truncate .... 1. *Bumelia*
    - ee. Corolla lobes without appendages; petioles 3–9 cm long, usually ½ the length of the blade or more .... 6. *Mastichodendron*
  - dd. Seed scar lateral, usually extending past the middle of the seed; stamen insertion various; corolla without dorsal or lateral appendages.
    - g. Leaves striate, the lateral veins usually less than 1 mm apart; seeds with some endosperm .... 7. *Micropholis*
    - gg. Leaves with 8–20(–50) lateral veins, usually 4 mm or more apart; seed without endosperm.
      - h. Sepals united for ½ their length or more .... 11. *Synsepalum*
      - hh. Sepals essentially free, imbricate or quincuncial .... 10. *Pouteria*
- cc. Flowers with staminodes irregularly present or rudimentary or lacking.
  - i. Seed without endosperm.
    - j. Seed scar lateral, linear, 3 mm or less in width; corolla lobes generally as long as the tube.

k. Ovary 1–3-loculed; leaves often glaucous, the lateral veins 13–18 pairs, weak or obscure beneath .... 9. *Neoxythece*
kk. Ovary (4–)5(–6)-loculed; leaves not glaucous, the lateral veins 7–11 pairs, well developed .... 10. *Pouteria*
jj. Seed scar lateral, covering ½ of seed, elliptic or oblong, 1 cm or more wide; corolla lobes more than twice as long as the tube .... 4. *Elaeoluma*
ii. Seed with endosperm .... 2. *Chrysophyllum*

1. BUMELIA

Bumelia Swartz, Prodr. Veg. Ind. Occ. 49. 1788, nom. cons. TYPE: *B. retusa* Swartz.

Shrubs or trees usually armed with spines. *Leaves* alternate, exstipulate; blades firm. *Flowers* subsessile to pedicellate; sepals 5, uniseriate; corolla lobes 5, each lobe entire or divided into 3 segments; stamens epipetalous, the filaments attached at the level of the sinuses, the staminodes alternating with the stamens, petaloid, entire to erose or lacinate; ovary 5-loculed. *Fruit* baccate, rounded to retuse at the apex; seeds solitary, the seed scar subbasal, small, scarcely longer than broad, the endosperm absent, the cotyledons fleshy.

Bumelia is a genus of about 25 species found in tropical and warm America.

Literature:

Cronquist, A. 1945. Studies in the Sapotaceae, III. *Dipholis* and *Bumelia*. J. Arnold Arbor. 26: 435–471 (*Bumelia*, 445–471).

1. **Bumelia persimilis** Hemsley subsp. **persimilis**, Biol. Centr.-Amer., Bot. 2: 298. 1882. TYPE: Mexico, Vera Cruz, Orizaba, *Botteri 989* (F, US, isotypes).

Shrub or tree to 18 m. *Leaves* 3–12 cm long, 1–5 cm wide, usually elliptic, acute to obtuse; primary lateral veins 10–30 pairs; petiole 2–10 mm. *Flowers* several to numerous in the axils; pedicels 3–6 mm long; sepals (4–)5(–6), 1.8–3.7 mm long; corolla 4.5–6 mm long, the lobes 5, twice as long as the tube; filaments attached at the level of the sinuses; ovary 5-loculed. *Fruit* fleshy, smooth, 1.2–2.5 cm long, 1–2 cm wide, 1-seeded; seed scar small, subbasal (Blackwell, 1968).

This variety ranges from Mexico through Central America to Venezuela.

COCLÉ: El Valle de Antón along Río Indio trail, *Hunter & Allen 298* (EAP, F). LOS SANTOS: Los Santos, *Lao 321* (MO). PANAMÁ: Chepo, *Kluge 12* (US).

2. CHRYSOPHYLLUM

Chrysophyllum L., Sp. Pl. 192. 1753. TYPE: *C. cainito* L.

Trees or shrubs lacking spines. *Leaves* alternate, exstipulate; blades firm to coriaceous, the secondary lateral veins often parallel to the primary series. *Flowers* pedicellate; sepals 5, uniseriate; corolla lobes 5, lacking appendages; stamens epipetalous, the filaments variously attached from near the base of the corolla tube to the level of the sinuses, the staminodes absent or (rarely in individual flowers) 1 or more irregularly developed in the corolla sinuses; ovary 4–12-loc-

uled. *Fruit* baccate, often edible; seeds 1–several, the seed scar large, lateral or basilateral, variously developed, linear to covering nearly half the seed surface, the endosperm copious, the cotyledons thin and foliaceous.

Chrysophyllum is a pantropical genus of about 80 species.

Literature:

Aubréville, A. 1961. Notes sur les Sapotacées Africaines et Sud-Américaines. Adansonia, n.s., 1: 6–38 (*Chrysophyllum*, 9–13).

Cronquist, A. 1945. Studies in the Sapotaceae, I. The North American species of *Chrysophyllum*. Bull. Torrey Bot. Club 72: 191–204.

———. 1946. Studies in the Sapotaceae, V. The South American species of *Chrysophyllum*. Bull. Torrey Bot. Club 73: 286–311.

a. Corolla lobes equal to or longer than the tube; sepals to 1 mm long.
- b. Seed scar lateral, nearly as long as the seed, 4–7 mm wide; stigma lobes mostly 7–12; fruit 4–10-seeded .... 1. *C. cainito*
- bb. Seed scar basilateral, nearly as broad as long, not reaching much past middle of the seed or shorter; stigma lobes (4–)5(–6); fruit 1-seeded .... 4. *C. mexicanum*

aa. Corolla lobes generally less than half as long as the tube; sepals 1–4 mm long.
- c. Sepals 1–2 mm long; seed scar basilateral, not reaching much past middle of seed, usually shorter .... 5. *C. panamense*
- cc. Sepals 3–4 mm long.
  - d. Staminal filaments attached near the middle of the corolla tube; pedicel to 5 mm long; petiole 1–3 cm long; seed scar lateral, nearly entire length of seed .... 2. *C. excelsum*
  - dd. Staminal filaments attached to the top of the corolla tube; pedicel 4–20 mm long; petiole 1 cm or less in length; seed scar presumably basilateral, reaching only middle of seed .... 3. *C. hirsutum*

1. **Chrysophyllum cainito** L., Sp. Pl. 192. 1753.

Tree to 30 m. *Leaves* 10–16 cm long, 5–8 cm wide, elliptic to oblong, short-acuminate; primary lateral veins 10–18 pairs; petioles 1–2.5 cm long. *Flowers* numerous in the axils; pedicels 5–16 mm long; sepals (4–)5(–6), ca. 1 mm long; corolla 3–5 mm long, the lobes (4–)5(–6), as long as the tube or slightly longer; filaments attached at the level of the sinuses; ovary 4–12-loculed. *Fruit* fleshy, subglobose, 3–10 cm broad, 4–10-seeded; seed scar lateral, extending nearly as long as the seed, elliptic, 4–7 mm broad (Blackwell, 1968).

Chrysophyllum cainito ranges over Mexico through Central America to northern South America and from Florida through the West Indies. It is widely cultivated and is probably indigenous only to the West Indies.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 24* (F). Almirante, road to Chiriquí, *McDaniel 5074* (MO). Chiriquí Lagoon, *Wedel 2523* (MO). CANAL ZONE: Ancón Hill, *Allen 2672* (EAP). Madden Dam and along Azote Caballo Road near Alajuela, *Dodge 16573* (MO, UC). Upper Chilibre River, ½–1 mi below Chilibre, *Seibert 1505* (MO). CHIRIQUÍ: E of Gualaca, *Allen 5033* (EAP, MO). Progreso, *Cooper & Slater 247* (F), *264* (F). Burica Peninsula, San Bartolo Limite, 12 mi W of Puerto Armuelles, *Croat 22168* (MO). COCLÉ: Floor of El Valle de Antón, *Allen 2747* (EAP, F). DARIÉN: Río Sabana above Santa Fé, *Duke 14104* (MO). Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 853* (MO, UC). HERRERA: Ocú, *Allen 3647* (EAP, MO). LOS SANTOS: Tonosí, *Duke 12488* (MO). PANAMÁ: Panamerican Highway ca. halfway between El Llano and Río Momoní, *Duke 5527* (MO). Chepo, *Kluge 49* (F). Taboga Island, *Woodson et al. 1537* (MO). SAN

BLAS: Mainland opposite Playon Chico, *Gentry 6397* (MO). VERAGUAS: Cerro Tute, region W of Santa Fé, *Allen 4441* (EAP, MO). Coiba Island, *Dwyer 2331* (MO). El Embalsadero, 8 mi W of Santiago, *Tyson 6075* (MO).

2. **Chrysophyllum excelsum** Huber, Bol. Mus. Paraense Hist. Nat. 3: 55. 1902. TYPE: Brazil, specimens collected from a cultivated tree at Pará, *Huber 3016* (G, not seen; F, US, isotypes).

Tree to 30 m. *Leaves* with petioles 1–4 cm long; blades elliptic to elliptic-obovate, thin to firm, rounded to mucronate, 6–30 cm long, 4–12 cm wide, glabrate; primary lateral veins 9–14 pairs, the secondary and tertiary ones forming an evident reticulum. *Flowers* 5–10 at recently defoliated nodes; pedicels 3–5 mm long, strigose; sepals 5, ovate, 3–3.5 mm long, 3–4 mm wide, rufous sericeous-strigose; corolla 3.8–4.3 mm long, the lobes 5, fringed-ciliolate, ca. ¼ as long as the tube; filaments attached near the middle of the tube; ovary 5-loculed, the style 0.5–2.5 mm long, glabrous. *Fruit* yellow, globose, 3.5–5 cm thick; seeds 4–5, ovoid, about 25 mm long, 13–14 mm wide, 7 mm thick, the seed scar lateral, as long as the seed, ovate, 2–5 mm broad.

This species occurs in the upper Amazon Basin, Brazil, Venezuela, and Panama.

Leaves of the Panamanian material are generally thicker and smaller than those found on South American plants, but the venation pattern is very similar and otherwise the plants are not distinctive.

PANAMÁ: Near archeological site at edge of Madden Lake, *Gentry & Tyson 5040* (MO).

3. **Chrysophyllum hirsutum** Cronquist, Bull. Torrey Bot. Club 72: 198. 1945. TYPE: Costa Rica, Alajuela, Villa Quesada, San Carlos, edge of forest, *Austin Smith 1776* (A, not seen; F, isotype).

Shrub or tree to 10 m tall. *Leaves* with petioles to 1 cm long; blades generally elliptic, thin, rounded to abruptly acuminate, 6–11 cm long, 2.5–5 cm wide, sparsely rufous-hirsutulose, glabrate; primary lateral veins 10–15 pairs, the secondary and tertiary ones inconspicuous. *Flowers* 2–6 in the axils; pedicels 4–20 mm long, sericeous-strigose; sepals 5, acute to rounded, 2–4 mm long, 1.5–2.5 mm wide, densely rufous pubescent; corolla greenish white, 4.5–7 mm long, rufous pubescent on the back of the lobes and distal portion of the tube, the lobes (4–)5, ⅓–½ as long as tube; filaments to 0.5 mm long, attached at the level of the sinuses; ovary densely rufous pubescent, 5-loculed. *Fruit* little known, but apparently 1-seeded and over 2 cm long.

This species occurs in Costa Rica and Panama.

Chrysophyllum hirsutum is known from moist forest at elevations over 600 m. The pedicels of Panamanian material are two to three times longer than those collected from Costa Rica, but otherwise the plants are not distinctive.

COLÓN: Agua Clara rainfall station, Santa Rita Ridge, *Foster 1739* (MO). Santa Rita Ridge, *Gentry & Dwyer 4800* (MO). PANAMÁ: Cerro Azul, *Lao & Holdridge 34* (MO).

4. **Chrysophyllum mexicanum** Brand. ex Standley, Contr. U.S. Natl. Herb. 23: 1114. 1924. TYPE: Mexico, Veracruz, Zacuapán, *Purpus 7679* (US, holotype; MO, NY, UC, isotypes).

Shrub or tree to 20 m tall. *Leaves* with petioles 4–10 mm long; blades generally elliptic, thin, acuminate to acute, 5–14 cm long, 2–6 cm wide, rufous to pale pubescent, glabrate; primary lateral veins 9–14(–20) pairs, prominent to very weak, the secondary and tertiary ones weak and often obscure. Flowers 1–15 (–20) in the axils; pedicels 2–5 mm long, pale to rufous pubescent; sepals 5, ovate, ca. 1 mm long, 1 mm wide, rufous or pale pubescent; corolla greenish white, 2–2.5(–3.5) mm long, glabrous, the lobes (4–)5, as long as the tube or slightly longer; filaments 0.1–0.5 mm long, attached near the level of the sinuses; ovary rufous pubescent, 5–6-loculed, the stigma 0.1–0.4 mm long, 5–6-lobed. *Fruit* ellipsoid, 1.5–2 cm long, 1 cm thick, smooth, glabrate; seeds solitary, ovoid, ca. 12 mm long, 7–8 mm thick, the seed scar basilateral, extending to about the middle of the seed, 3–4 mm broad.

This species ranges from Mexico through Central America to Colombia.

Chrysophyllum mexicanum is highly variable as to leaf size, pubescence, and degree of prominence of the lateral veins, but these differences are not sufficiently correlated to justify the recognition of subspecies or varieties.

COCLÉ: El Valle de Antón, *Croat 25282* (MO); *Lao 286* (MO). Behind Club Campestre, *Duke 13266* (MO). DARIÉN: Hills near Pidiaque, *Duke 8047* (MO). Río Sabana above Santa Fé, *Duke 14108* (MO).

5. **Chrysophyllum panamense** Pittier, Contr. U.S. Natl. Herb. 18: 165. 1916. TYPE: Panama, *Pittier 4005* (US, holotype; NY, isotype).

Tree to 15 m. *Leaves* 15–25 cm long, 6–11 cm wide, elliptic to elliptic-obovate, acuminate; primary lateral veins 10–20 pairs; petioles 1–2.5 cm long. *Flowers* several to numerous in the axils; pedicels 3–7 mm long; sepals (4–)5(–6), 1–2 mm long; corolla 3.5–6 mm long, the lobes (4–)5(–6), less than ½ the length of the tube; filaments attached at the level of the sinuses; ovary 4–12-loculed. *Fruit* fleshy, subglobose to ovoid, to 2 cm broad, 3–8-seeded; seed scar basilateral, extending to the middle of the seed or slightly beyond (Blackwell, 1968).

This species occurs in Costa Rica, Panama, and Venezuela (Amazonas).

BOCAS DEL TORO: Almirante, *Cooper 353* (F). Without locality, *Wedel 230* (F, MO). CANAL ZONE: Barro Colorado Island, *Aviles 969* (F); *Bailey & Bailey 397* (F); *Croat 8012* (MO); *Ebinger 210* (MO); *Gangham 591* (F); *Hayes s.n.* (F, MO); *Shattuck 778* (F), *969* (MO), *1024* (F, MO); *Starry 82* (F), *118* (F); *Wetmore & Abbe 169* (F); *Zetek 3810* (EAP, F, MO), *4327* (F), *4330* (F). Sirri River, Trinidad Basin, *Pittier 4005* (NY, US). COLÓN: Between Salud and Boca del Río Indio, *Howell 28* (MO). 2–3 mi up Río Guanche, *Kennedy & Foster 2153a* (MO). Río Viejo, 4 km NE of Puerto Pilón, *Nee 7178* (MO). DARIÉN: La Boca de Pirre, *Bristan 1271* (MO). PANAMÁ: El Llano-Cartí Road, 2.3 km N of Panamerican Highway, *Nee & Dwyer 9239* (MO).

3. DIPHOLIS

Dipholis A. DC. in DC., Prodr. 8: 188. 1844, nom. cons. TYPE: *D. salicifolia* (L.) A. DC.

Trees or shrubs lacking spines or thorns. *Leaves* alternate, exstipulate; blades coriaceous. *Flowers* small, subsessile to pedicellate; sepals 5, uniseriate; corolla lobes 5, each lobe divided into 3 segments; stamens epipetalous, the filaments attached at the level of the sinuses, the staminodes alternating with the stamens, petaloid, often erose, fimbriate or lacinate; ovary 5-loculed. *Fruit* baccate, abruptly tapering to a short persistent style; seeds solitary, the seed scar basal, rarely basilateral, small, scarcely longer than broad, the endosperm copious, the cotyledons thin and foliaceous.

Dipholis is a tropical North American genus of about 15 species found principally in the Greater Antilles.

Literature:

Cronquist, A. 1945. Studies in the Sapotaceae, III. *Dipholis* and *Bumelia*. J. Arnold Arbor. 26: 435–471 (*Dipholis*, 435–445).

1. **Dipholis minutiflora** Pittier, Contr. U.S. Natl. Herb. 13: 464. 1912. TYPE: Costa Rica, Dota Mts., forests of El Copey, *Tonduz 11935* (US, holotype; NY, isotype).

Tree to 30 m. *Leaves* 5–20 cm long, 2–10 cm wide, elliptic-oblanceolate to elliptic-obovate, rounded to acute; primary lateral veins 10–20 pairs; petiole 5–18 mm long. *Flowers* numerous at defoliated nodes; pedicels 3–10 mm long; sepals 5(–8), 1.5–2.2 mm long; corolla 4–4.5 mm long, the lobes 5, twice as long as the tube; filaments attached at the level of the sinuses; ovary 5-loculed. *Fruit* 1.5–2.5 cm long, 1–2 cm wide, the flesh scant, wrinkled when dry; seed solitary, the seed scar subbasal, broadly elliptic, 3–5 mm long (Blackwell, 1968).

This species ranges from Mexico to Panama.

CHIRIQUÍ: Cerro Punta, *Allen 1564* (EAP, F, MO). Quebrada Velo, Finca Lerida, *Allen 4676* (EAP, MO). Valley of the upper Río Chiriquí Viejo, *White 109b* (F, MO); *White & White 1* (MO). Bajo Mono, mouth of Quebrada Chiquero, along Río Caldera, *Woodson et al. 995* (F, MO). PANAMÁ: Hills above Campana, *Allen 1314* (EAP, F, MO). Cerro Jefe, *Gentry 4867* (MO).

4. ELAEOLUMA

Elaeoluma Baillon, Hist. Pl. 11: 293. 1892. TYPE: *E. schomburgkiana* (Miq.) Baillon.

Shrubs or small trees lacking spines. *Leaves* alternate, exstipulate; blades firm to coriaceous, the primary lateral veins generally few. *Flowers* short pedicellate; sepals 5, uniseriate; corolla lobes 5, lacking appendages; stamens epipetalous, the filaments attached to a very short corolla tube, the staminodes alternating with the stamens, rudimentary, the number irregular, often completely absent; ovary (2–)3(–5)-loculed. *Fruit* baccate; seeds solitary, the seed scar lateral, linear to very broad, the endosperm absent, the cotyledons fleshy.

Elaeoluma is a genus of 3 species found chiefly in northern South America.

1. **Elaeoluma glabrescens** (Mart. & Eichl.) Aubréville, Adansonia, n.s., 1: 26. 1961.

Lucuma glabrescens Mart. & Eichl. in Mart., Fl. Bras. 7: 72. 1863. TYPE: Brazil, Rio Negro between Barcellos and San Gabriel, *Spruce 2029* (photo MO; NY, P, isotypes).

Tree of unknown height. *Leaves* with petioles 10–15 mm long; blades ovate-elliptic to oblong-elliptic, firm to coriaceous, acuminate, 7–15 cm long, 3–7 cm wide, glabrous; primary lateral veins 9–12 pairs, slender, obscure above, slightly raised and evident beneath, the secondary and tertiary ones closely anastomosing. *Flowers* 5–10 in the axils or at recently defoliated nodes; pedicels 3–5 mm long; sepals 5(–6), ovate, 2–6 mm long, glabrate; corolla glabrous, 5–6 mm long, the lobes 5, elliptic, 3–5 times longer than the tube; filaments to 1.5 mm long, attached to the very short tube, the staminodes not observed; ovary pilose to minutely tomentose, (2–)3(–5)-loculed, the style 1–2 mm long, glabrous. *Fruit* obovoid to subglobose, smooth, glabrous, 2–4.5 cm long, 1–3 cm wide; seeds solitary, ovoid to obovoid, to 3 cm long, 2.5 cm wide, the seed scar covering about half the seed, ventral, extending the entire length.

This species occurs in Amazonian Brazil, Peru, and Panama.

Elaeoluma glabrescens is closely related to species of *Neoxythece*, but it is readily distinguished by its broad, ventral seed scar. The number of ovary locules has been used to separate these genera, but I have found it to be too variable to be useful in identifying specimens.

SAN BLAS: Chucunaque, 2–10 mi above the Cuna-Darién boundary, *Duke 8565* (MO).

5. MANILKARA

Manilkara Adanson, Fam. Pl. 2: 166. 1763, nom. cons. TYPE: *M. kauki* (L.) Dubard.

Trees lacking spines. *Leaves* alternate, exstipulate; blades coriaceous; primary lateral veins numerous, fine. *Flowers* long-pedicellate; sepals 6, biseriate; corolla lobes 6, each lobe often divided into 3 segments; stamens epipetalous, the filaments attached at the level of the sinuses, the staminodes alternating with the stamens, petaloid, rarely replaced by functional stamens; ovary 6–16-loculed. *Fruit* baccate; seeds 1–several, ovoid to laterally compressed, the seed scar basilateral, oval to linear, the endosperm copious, the cotyledons thin and foliaceous.

Manilkara is a pantropical genus of about 50 species.

Literature:

Cronquist, A. 1945. Studies in the Sapotaceae, IV. The North American species of *Manilkara*. Bull. Torrey Bot. Club 72: 550–562.

a. Corolla lobes with broad dorsal appendages, appearing to be 18 in number.
  b. Flowers 3–12 per axillary fascicle; pedicel glabrous; fruit smooth or slightly roughened; seed solitary, the scar 5 mm broad, basilateral, barely reaching middle of seed .... 1. *M. bidentata*

bb. Flowers solitary in the leaf axils; pedicel tomentulose to glabrate; fruit mealy roughened; seeds several, the scar 2 mm broad, linear, from near the base to well beyond the middle of the seed .... 3. *M. meridionalis*

aa. Corolla lobes entire or merely tridentate at the apex, appearing to be 6 in number.

c. Flowers 2–5 per axillary fascicle; pedicel strigillose; corolla tube less than half as long as the lobes; seed scar basilateral, linear, barely reaching the middle of the seed .... 2. *M. chicle*

cc. Flowers solitary in the leaf axils; pedicel rufous-tomentulose; corolla tube more than half as long as the lobes; seed scar linear, from near the base to well beyond the middle of the seed .... 4. *M. zapota*

1. **Manilkara bidentata** (A. DC.) Chevalier, Rev. Int. Bot. Appl. Arg. Trop. 12: 270. 1932.

Mimusops bidentata A. DC. in DC., Prodr. 8: 204. 1844. TYPE: French Guiana, *Richard* (not seen).

Tree to 35 m. *Leaves* 6–30 cm long, 3–12 cm wide, obovate to elliptic, obtuse to emarginate; petioles 1.5–4 cm long. *Flowers* 3–12 in the axils or at recently defoliated nodes; pedicels 1.2–3 cm long; sepals 4–6 mm long; corolla 5–7 mm long, the tube ca. $^1/_5$ of the total length, the lobes with 2 dorsal appendages as broad as and slightly longer than the lobes; ovary 6–10-loculed. *Fruit* smooth or slightly roughened, subglobose, 2–3.5 cm long, 1-seeded; seed scar basilateral, barely reaching the middle of the seed, ca. 5 mm broad (Blackwell, 1968).

This species occurs in Hispaniola, Puerto Rico, Lesser Antilles, northern South America and Panama.

BOCAS DEL TORO: Río San Pedro, between the Río Caña and Río Calovébora, *Gordon 13* (MO). Without locality, *Cox s.n.* (US). CANAL ZONE: Hills around Gatún, *Pittier 2699* (US). PANAMÁ: Chepo, *Kluge 55* (EAP, US). SAN BLAS: Hills near Puerto Obaldía, *Pittier 4318* (NY, US), *4384* (US).

2. **Manilkara chicle** (Pittier) Gilly, Trop. Woods 73: 14. 1943.

Achras chicle Pittier, J. Wash. Acad. Sci. 9: 436. 1919. TYPE: Guatemala, Izabal, Vega Grande, near Los Amates, *Pittier 8537* (US, holotype; NY, isotype).

Tree to 40 m. *Leaves* 8–26 cm long, 3–8 cm wide, oblanceolate to elliptic, rounded to acuminate; petioles 1–3.5 cm long. *Flowers* 2–5 in the axils; pedicels 0.5–3 cm long; sepals 5–9 mm long; corolla 5.5–9 mm long, the tube $^1/_6$–$^1/_3$ of the total length, the lobes without dorsal appendages; ovary 7–9-loculed. *Fruit* mealy roughened, subglobose, 2–4 cm long, 4–6-seeded; seed scar basilateral, barely reaching middle of the seed, narrow, 2 mm wide (Blackwell, 1968).

This species ranges from Mexico through Central America to Colombia.

CANAL ZONE: Ancón Hill, *Standley 26384* (US). COCLÉ: La Pintada, *Léon 22* (MO). COLÓN: Santa Rita Ridge, *Gentry 6566* (MO). Santa Rita Ridge Road, 17 km from Boyd-Roosevelt Highway, *Mori & Kallunki 5031* (MO). DARIÉN: Piñas, *Duke 10653* (MO). Patiño, *Pittier 5698* (US). LOS SANTOS: Ca. ½ mi S of Pedasí, *Stimson 5294* (MO, UC). PANAMÁ: Trapiche Island, *Allen 2607* (EAP). San José Island, *Johnston 342* (MO), *753* (MO, US). Cerro Peñón, 3 km S of Alcalde Díaz, *Nee 8867* (MO). Around Alhajuela, Chagres Valley, *Pittier 3457* (US).

3. **Manilkara meridionalis** Gilly, Trop. Woods 73: 12. 1943. TYPE: Costa Rica, Punta Arenas, Esparta, *Biolley 17308* (US, holotype; NY, isotype).

Tree to 30 m. *Leaves* 5–13 cm long, 1.5–4.5 cm wide, elliptic to narrowly obovate, rounded to acuminate; petioles 1–2.7 cm long. *Flowers* solitary in the axils; pedicels 1–2.3 cm long; sepals 6–9 mm long; corolla 7–10 mm long, the tube ½–⅔ of the total length, the lobes with 2 dorsal appendages broader than but about equal in length to the lobes; ovary 9–12-loculed. *Fruit* mealy roughened, subglobose, 3–3.5 cm long, several seeded; seed scar basilateral, extending past the middle of the seed, linear, 2 mm wide (Blackwell, 1968).

This species ranges from Mexico through Central America to Colombia and Venezuela.

PANAMÁ: Taboga Island, *Standley 27099* (US); *Woodson et al. 1455* (MO, NY). Without locality, *Hayes 793* (NY).

4. **Manilkara zapota** (L.) van Royen, Blumea 7: 410. 1953.

Achras zapota L., Sp. Pl. 2: 1190. 1753, based on *Sapota fructu ovato, majori* Plumier.
Sapota fructu ovato, majori Plumier, Nov. Pl. Amer. Gen. 43, *tab. 4.* 1703. TYPE: Plumier's plate, for discussion see Moore & Stearn, Taxon 16: 382–395. 1967.

Tree to 40 m. *Leaves* 4–15 cm long, 1.5–6 cm wide, elliptic to oblong-elliptic, rounded to acuminate; petioles 0.8–3 cm long. *Flowers* solitary in the axils; pedicels 1.2–2.5 cm long; sepals 6–10 mm long; corolla 6–11 mm long, the tube ½–⅔ of the total length, the lobes without dorsal appendages; ovary 10–12-loculed. *Fruit* mealy roughened, subglobose, to 10 cm in diameter, (4–)8–12-seeded; seed scar basilateral, extending well past the middle of the seed, linear, 2 mm wide (Blackwell, 1968).

This species ranges from Mexico through Central America to northern South America and from Florida through the West Indies. It is widely cultivated and many collections represent introduced plants.

CANAL ZONE: Summit Gardens, *Croat 6760* (MO); *Mori & Kallunki 1875, 4532* (both MO). Balboa, *Standley 27121* (MO, US), *30860* (US).

6. MASTICHODENDRON

Mastichodendron Cronquist, Lloydia 9: 245. 1946. TYPE: *M. foetidissimum* (Jacq.) Cronquist.

Trees lacking spines. *Leaves* alternate to subopposite, exstipulate; blades firm, the primary lateral veins few, curved. *Flowers* pedicellate; sepals 5, uniseriate; corolla lobes 5, lacking appendages; stamens epipetalous, the filaments attached near the level of the sinuses, the staminodes alternating with the stamens, ovate to deltoid or lanceolate, not petaloid; ovary 5-loculed. *Fruit* baccate; seeds solitary, the seed scar basilateral, circular to lanceolate, not extending past the middle of the seed, the endosperm copious, the cotyledons thin and foliaceous.

Mastichodendron is a tropical North American genus of about 6 species.

Literature:

Cronquist, A. 1946. Studies in the Sapotaceae, II. Survey of the North American genera. Lloydia 9: 241–292 (*Mastichodendron*, 244–252).

1. **Mastichodendron capiri** (A. DC.) Cronquist var. **tempisque** (Pittier) Cronquist, Lloydia 9: 250. 1946.

Sideroxylon tempisque Pittier, Contr. U.S. Natl. Herb. 13: 461. 1912. TYPE: El Salvador, La Laguna de Santa Tecla, *Pittier 1917* (US).

Tree to 25 m. *Leaves* 6–15 cm long, 3–7 cm wide, generally elliptic, acuminate to rounded (emarginate); primary lateral veins 8–15 pairs; petioles 3–9 cm long. *Flowers* numerous at defoliated nodes; pedicels 3–8 mm long; sepals 5, 1.5–3.2 mm long; corolla 5–8 mm long, the lobes 5, twice as long as the tube; filaments attached at the level of the sinuses; ovary 5-loculed. *Fruit* yellow, 2.5–4 cm long, 2–3 cm wide, 1-seeded, the flesh scant, wrinkled when dry; seed scar basilateral, lanceolate to subglobose, 6–9 mm long, 4–6 mm wide (Blackwell, 1968).

This species ranges from Mexico through Central America to Panama.

COCLÉ: Penonomé, *Williams 421* (F, NY, US). LOS SANTOS: Corozal de Macaracas, *Lao 588* (MO).

7. MICROPHOLIS

Micropholis Pierre, Not. Bot. Sapot. 37. 1891. TYPE: *M. rugosa* (Swartz) Pierre.

Trees or shrubs lacking spines. *Leaves* alternate, exstipulate; blades firm, appearing striate, the primary lateral veins numerous, fine, crowded, nearly straight. *Flowers* pedicellate; sepals 5, uniseriate; corolla lobes 5, lacking appendages; stamens epipetalous, the filaments attached near the level of the sinuses, the staminodes alternating with the stamens, lanceolate to subpetaloid; ovary 5-loculed. *Fruit* baccate; seeds 1–several, the seed scar lateral, linear, the endosperm present but not copious, the cotyledons fleshy.

Micropholis is a tropical American genus of about 30 species.

Literature:

Cronquist, A. 1946. Studies in the Sapotaceae, II. Survey of the North American genera. Lloydia 9: 241–292 (*Micropholis*, 252–257).

1. **Micropholis mexicana** Gilly ex Cronquist, Lloydia 9: 257. 1946. TYPE: Mexico, Chiapas, Mt. Ovando, Escuintla, *Matuda 4195* (F, K, MO, NY).

Tree to 20 m. *Leaves* with petioles 8–10 mm long, highly canaliculate; blades narrowly elliptic to elliptic-obovate, thin, abruptly acuminate, 10–15 cm long, 3–5 cm wide, essentially glabrous; primary lateral veins very numerous and fine, 0.2–0.3 mm apart. *Flowers* 5–10(–30) in the axils or at recently defoliated nodes; pedicels 4–8 mm long, rufous puberulent; sepals 5(–6), broadly ovate, 2.5–3.5 mm long, 2.5 mm wide, rufous pubescent abaxially, glabrous on the inner surface;

corolla white, glabrous, 5–6.5 mm long, the lobes 5, ovate, as long as or slightly longer than the tube; filaments 1–1.8 mm long, attached at the level of the sinuses, the staminodes 5, lance-subulate, 1.5–3 mm long; ovary rufous pubescent, 5-loculed, the style 5–6 mm long, glabrous. *Fruit* broadly ellipsoidal to pyriform, 2–3.5 cm long; seeds solitary, ellipsoidal, laterally compressed, 20–25 mm long, the seed scar linear, extending the length of the seed, to 5 mm wide.

This species occurs in Mexico, Belize and Panama.

The disjunct distribution of *Micropholis mexicana* is noteworthy, and Standley & Williams (Fieldiana, Bot. 24: 232. 1967) mention an apparently undescribed Panamanian species. However, I find no specific differences in the material from Panama.

PANAMÁ: Cerro Jefe, *Foster & Kennedy 1871* (MO). El Llano-Cartí road, 12 km from Panamerican Highway, *Mori et al. 4668* (MO).

8. MIMUSOPS

Mimusops L., Sp. Pl. 349. 1753. TYPE: *M. elengi* L.

Trees lacking spines. *Leaves* alternate; stipules caducous; blades glabrous or soon glabrate. *Flowers* pedicellate; sepals 8, biseriate; corolla lobes 8, each lobe divided into 3 segments; stamens epipetalous, the filaments attached at the level of the sinuses, the staminodes alternating with the stamens, usually simple, lanceolate or ligulate, densely pilose abaxially and along the margins; ovary usually 8-loculed. *Fruit* baccate; seeds 1–several, ovoid to laterally compressed, the seed scar basal to basilateral, scarcely longer than broad, the endosperm copious, the cotyledons thin and foliaceous.

A genus of about 40 species found throughout the Old World tropics. Two species are cultivated in Panama.

a. Pedicels 40–70 mm long; leaves thick, the petioles 1–1.5 cm long, the primary lateral veins 8–10 pairs .... 1. *M. commersonii*
aa. Pedicels 7–8 mm long; leaves thin, the petioles 2–2.6 cm long, the primary laterals 15–25 pairs .... 2. *M. elengi*

1. **Mimusops commersonii** (G. Don) Engler, Monogr. Afrik. Pflanzen-Fam. 8: 77. 1904.

Imbricaria commersonii G. Don, Gen. Syst. 4: 35. 1838. TYPE: Madagascar, *Commerson* (P).

Tree to 20 m. *Leaves* with petioles 1–1.5 cm long; blades obovate to elliptic, thick, rounded to emarginate, (7–)10–13(–20) cm long, (4–)6–8(–11) cm wide, densely rufous pubescent, soon glabrate; primary lateral veins 8–10 pairs, the secondary ones parallel to the primary laterals and nearly the same size, the tertiary laterals irregularly anastomosing. *Flowers* 1–3 in the axils or at recently defoliated nodes; pedicels 4–7 cm long, stout, rufous pubescent; sepals 7–12 mm long, lanceolate, densely rufous pubescent; corolla glabrous, 7–13 mm long, the lobes 6–11 mm long with 2 dorsal appendages frequently divided 2–5 times, the tube 1–2 mm long; filaments 0.5–3.5 mm long, attached at the level of the sinuses, the staminodes lanceolate, 4–6 mm long, rufous pubescent; ovary densely rufous

pubescent, 8-loculed, the style 5–6 mm long. *Fruit* globose, 3–5 cm in diameter; seeds 2–8, laterally compressed, 2–2.5 cm long, the seed scar basal, nearly circular, 5 mm broad.

This species occurs in Madagascar and the Comores. It is cultivated in Panama and elsewhere in the tropics. The edible pulp of the fruit is reputedly mealy and sweet.

CANAL ZONE: Summit Garden, *Hayes 305* (US). VERAGUAS: Divisa, *Lao 4* (MO).

2. **Mimusops elengi** L., Sp. Pl. 349. 1753.

Tree to 15 m. *Leaves* with petioles 2–2.6 cm long; blades elliptic to elliptic-obovate, thin, 5–12 cm long, 4–6 cm wide, sparsely rufous pubescent, soon glabrate; primary lateral veins 15–25 pairs, fine, the secondary ones parallel to the primary laterals and nearly the same size, the tertiary laterals irregularly anastomosing. *Flowers* 1–3 in the axils; pedicels 7–8 mm long, rufous pubescent; sepals 6–7 mm long, triangular, pale rufous pubescent; corolla white, glabrous, 8–12 mm long, the lobes 6–9 mm long with 2 dorsal appendages of about equal length, the tube 2–4 mm long; filaments 1–3 mm long, attached at the level of the sinuses, the staminodes lanceolate, 4–6 mm long, pubescent; ovary densely pubescent, 8-loculed, the style 3–4 mm long. *Fruit* ovoid, smooth, 2–3 cm long, 1.5–2 cm thick; seeds solitary, ovoid, 1.5–2 cm long, the seed scar basilateral, nearly circular, 3 mm broad.

This species is from southeast Asia. It is cultivated in Panama and elsewhere in the tropics. It is a good shade tree with sweetly scented small white flowers.

CANAL ZONE: Coco Solo Navy Reservation, *Coffey s.n.* (MO). Cultivated street tree, *Nee 14035* (MO). Fort Clayton, *Tyson & Blum 2005* (MO). Curundu, *Tyson 3460, 3482* (both MO). PANAMÁ: Panama City, *Lao 455* (MO). Near Hotel Panama, *Nee 11492* (MO).

9. NEOXYTHECE

Neoxythece Aubréville & Pellegrin, Adansonia, n.s., 1: 16. 1961. TYPE: *N. elegans* (A. DC.) Aubréville.

Trees or shrubs lacking spines. *Leaves* alternate, exstipulate; blades firm to coriaceous, the primary lateral veins few, often obscure. *Flowers* short-pedicellate; sepals 5, uniseriate; corolla lobes 5, lacking appendages; stamens epipetalous, the filaments variously attached from near the base of the tube to the level of the sinuses, the staminodes alternating with the stamens, rudimentary, the number irregular, often completely absent; ovary 2(–3)-loculed. *Fruit* baccate; seeds solitary, the seed scar lateral, linear, usually extending nearly the entire length of the seed, the endosperm absent, the cotyledons fleshy.

Neoxythece is a tropical American genus of about 10 species found chiefly in northern South America.

Literature:

Cronquist, A. 1946. Studies in the Sapotaceae, VI. Miscellaneous notes. Bull. Torrey Bot. Club 73: 465–471 (*Oxythece*, 467–468).

a. Fruit constricted basally to a stipe 8–15 mm long, not beaked, yellow orange; leaves glabrous, rarely pale pubescent beneath .... 1. *N. dura*
aa. Fruit with a prominent beak to 1 cm long, not stipitate, purple black; leaves chestnut brown puberulent beneath .... 2. *N. maguirei*

1. **Neoxythece dura** (Eyma) Aubréville & Pellegrin, Adansonia, n.s., 1: 17. 1961.

Pouteria dura Eyma, Recueil Trav. Bot. Néerl. 33: 187. 1936. TYPE: Guyana, *Schomburgk 910* (not seen).

Tree to 8 m. *Leaves* with petioles 10–15 mm long; blades obovate to elliptic-obovate, firm to coriaceous, acute to rarely rounded, acuminate, 4–8 cm long, 2–3 cm wide, glabrous above, rarely pale puberulent beneath, glabrate; primary lateral veins 13–18 pairs, obscure, the secondary and tertiary ones obscure. *Flowers* 2–7 in the axils or at recently defoliated nodes; pedicels 5 mm long; sepals 5, ovate, 1–2 mm long, 1–2 mm wide, abaxially rufous pubescent; corolla glabrous, 3 mm long, the lobes 5, ovate, as long as the tube; filaments to 0.5 mm long, attached near the middle of the tube, the staminodes 0–5, minute, deltoid; ovary hirsute, 2-loculed, the style 3 mm long. *Fruit* constricted basally to a stipe 8–15 mm long, subglobose above the stipe, yellow orange, rufous pubescent, 3–5 cm long, 2–2.5 cm broad; seeds solitary, ovoid, laterally compressed, to 2.5 cm long, the seed scar linear, extending nearly the entire length of the seed, 1–2 mm wide.

This species occurs in Brazil (Amazonas), Surinam, Guyana, Venezuela, Colombia, and Panama.

Neoyxthece dura is very closely related to *N. maguirei*, but its yellow orange, basally constricted fruits, even when they are young, readily distinguish it from the purple black fruits of *N. maguirei*.

DARIÉN: Without locality, *Duke & Bristan 8336* (MO). PANAMÁ: Road between El Llano and Cartí-Tupile, 12 mi above Panamerican Highway, *Liesner 1328* (MO, NY, UC).

2. **Neoxythece maguirei** Aubréville, Mem. New York Bot. Gard. 23: 223. 1972. TYPE: Venezuela, Amazonas, Río Guainía, infrequent in Caño Pimichín below Pimichín, *Maguire & Wurdack 35614* (NY, holotype; NY, isotype).

Shrub or small tree to 6 m. *Leaves* with petioles 10–15 mm long, highly canaliculate; blades obovate to obovate-elliptic, coriaceous, rounded, often cuspidate, 6–8 cm long, 3–3.5 cm wide, glabrous above, distinctly chestnut brown puberulent beneath; primary lateral veins 14–18 pairs, slender, the secondary and tertiary ones obscure. *Flowers* 1–7 at recently defoliated nodes; pedicels 4–5 mm long; sepals 5, ovate, 1.5–2 mm long, 1.5–2 mm wide, abaxially sparsely pubescent; corolla white, glabrous, 3–3.5 mm long, the lobes 5, ovate, ca. as long as the tube; filaments to 0.5 mm long, attached near the middle of the tube, the staminodes not observed; ovary hirsute, 2-loculed, the style 0.5 mm long. *Fruit* with a prominent beak to 1 cm long, ovoid, black purple, rufous pubescent, 2.5–3 cm long, 1–1.5 cm wide; seeds solitary, ellipsoidal, 17 mm long, 8 mm wide, 5 mm thick, the seed scar linear, extending nearly the entire length of the seed, 1–1.5 mm wide.

This species occurs in Venezuela (Amazonas) and Panama.

Neoxythece maguirei is similar and presumably closely related to *N. dura*.

PANAMÁ: El Llano-Cartí Highway, 17–20 km N of El Llano, *Dressler 4630* (MO). El Llano-Cartí road, km 12, *Croat 26045* (MO).

10. POUTERIA

Pouteria Aublet, Hist. Pl. Guiane 1: 85. *pl. 33.* 1775. TYPE: *P. guianensis* Aublet.

Trees or shrubs lacking spines. *Leaves* alternate or rarely subopposite, exstipulate; blades membranous to coriaceous, the primary lateral veins generally few, strongly arcuate near the margin. *Flowers* sessile to long-pedicellate; sepals 4–12, spiral or in 1 or 2 series; corolla lobes 4–6, lacking appendages; stamens epipetalous, occasionally abortive, the filaments variously attached from near the base of the tube to the level of the sinuses, the staminodes alternating with the stamens, petaloid to rudimentary; ovary 1–10-loculed. *Fruit* fleshy, occasionally sclerotic; seeds 1–several, the seed scar lateral, linear to very broad, the endosperm absent, the cotyledons fleshy.

Pouteria is a genus of perhaps 100 species found chiefly in tropical America.

Pouteria has been viewed quite differently by various workers. Baehni (1942) considered it in a very broad sense and included over 300 distinct species. More recently Baehni (1965) split the genus somewhat, but his list of generic synonyms still includes over twenty names, and a list of probable synonyms adds twenty more. Aubréville (1965, 1972) and Lundell (1976) have adopted much narrower generic concepts. Following Aubréville's nomenclature the Panamanian *Pouteria* would be split into no fewer than nine genera.

Blackwell (1968) followed the system proposed by Cronquist (1946), and I follow roughly the same generic limits for American Sapotaceae, particularly *Pouteria*. This is done with the knowledge that several segregates of *Pouteria* are probably sound and deserve recognition at least at the subgeneric level. Otherwise we are left with a large but still poorly defined genus. Unfortunately many of the segregate genera themselves are poorly defined, being based on relatively few specimens. As more material is collected, the generic limits may have to be shifted. This is particularly true among American species. Large series of specimens exist for relatively few species, and the number of species only known from the type collection is large. If Panamanian *Pouteria* can be used as an example, 7 of 25 species are known from only the type specimen or type locality. Similarly many species lack complete descriptions of flowers and/or fruits. In this treatment flowers of three *Pouteria* species are adequately described for the first time.

Aubréville (1965, 1972) has proposed the most complete scheme for dividing *Pouteria* (sensu lato) into its narrower generic units. To aid those unfamiliar with his many important works, which are exclusively in French, I have included in this portion of the treatment the name adopted by Aubréville. When it is certain, this name has been placed in the synonymy along with the basionym. A few species are known from such scanty material that correct placement in Aubré-

ville's scheme is uncertain. It should be noted that only 3 of the 25 Panamanian *Pouteria* would be retained in this genus by Aubréville.

Literature:

Aubréville, A. 1961. Notes sur des Poutériées Américaines. Adansonia, n.s., 1: 150–191.

Baehni, C. 1942. Mémoires sur les Sapotacées, II. Le Genre *Pouteria*. Candollea 9: 147–476.

Cronquist, A. 1946. Studies in the Sapotaceae, II. Survey of the North American genera. Lloydia 9: 241–292 (*Pouteria*, 257–291).

Lundell, C. L. 1976. Studies of American plants, XII. Wrightia 5: 241–259 (Sapotaceae, 252–256).

a. Sepals 8–12, evidently spiralled, increasing in size centripetally.
  b. Fruit fleshy.
    c. Leaves with 20–50 primary lateral veins; pedicels to 2 mm long; sepals often emarginate; corolla lobes as long as the tube .... 19. *P. sapota*
    cc. Leaves with 12–20 primary lateral veins; pedicels 4–6 mm long; sepals entire or scarcely emarginate; corolla lobes much shorter than the tube .... 13. *P. fossicola*
  bb. Fruit woody.
    d. Leaves with 8–13 primary lateral veins; sepals thick and fleshy .... 8. *P. cooperi*
    dd. Leaves with 13–20 primary lateral veins; sepals thin .... 20. *P. sclerocarpa*
aa. Sepals 4–7, imbricate or quincuncial, about equal in length.
  e. Flowers sessile, the pedicels 2 mm long or less.
    f. Sepals 5–7; filaments attached at the level of the sinuses between the corolla lobes (unknown in *P. chiricana*).
      g. Corolla 6–8 mm long; sepals 6 or 7; corolla tube longer than the corolla lobes .... 20. *P. sclerocarpa*
      gg. Corolla 2.5–5.5 mm long; sepals 5; corolla tube shorter than the corolla lobes.
        h. Secondary lateral veins fine, close, sinuous but regularly disposed .... 23. *P. subrotata*
        hh. Secondary lateral veins rather coarse, irregularly disposed.
          i. Fruit ovoid to subglobose; sepals 2.5–5.5 mm long .... 10. *P. durlandii*
          ii. Fruit ellipsoid, narrowed to a stipitate base; sepals 2–2.6 mm long .... 6. *P. chiricana*
    ff. Sepals 4(–5); filaments attached at the middle or base of the corolla tube (unknown in *P. sambuensis*).
      j. Fruit fleshy.
        k. Fruit glabrous .... 2. *P. caimito*
        kk. Fruit conspicuously hairy .... 18. *P. sambuensis*
      jj. Fruit woody or gall-like.
        l. Fruit covered with hairy processes to 2 cm long; sepals 7–9 mm long; corolla 6–9 mm long .... 16. *P. neglecta*
        ll. Fruit glabrous to pubescent, but no long hairy processes; sepals 2.5–4 mm long; corolla 2.5–4 mm long .... 22. *P. stylosa*
  ee. Flowers pedicellate, at least some pedicels 3 mm or more in length.
    m. Corolla at least 7 mm long; largest sepals at least 4 mm long.
      n. Corolla glabrous externally; pedicels 3–8 mm long.
        o. Sepals 4.
          p. Primary lateral veins of the leaves well marked, easily distinguished from the secondary ones; petioles 1.5–2.5 cm long; style 5–6 mm long .... 5. *P. carabobensis*
          pp. Primary lateral veins difficult to distinguish from the secondary ones; petioles 1–1.5 cm long; style 6–11 mm long .... 9. *P. dominigensis*

oo. Sepals 5–6 .... 1. *P. buenaventurensis*
nn. Corolla sparsely sericeous-strigose externally; pedicels 8–15 mm long .... 4. *P. campechiana*
mm. Corolla less than 6.5 mm long; sepals less than 3.5 mm long.
q. Ovary with 1–3 locules.
r. Leaves glabrous or essentially so .... 25. *P. unilocularis*
rr. Leaves densely pubescent, at least beneath.
s. Pubescence pale; leaves with 9–14 primary lateral veins .... 24. *P. tarapotensis*
ss. Pubescence rufous; leaves with 15–22 primary lateral veins .... 3. *P. calistophylla*
qq. Ovary with 4 or more locules.
t. Sepals and corolla lobes generally 4-merous.
u. Leaves finely pale sericeous beneath .... 12. *P. euryphylla*
uu. Leaves sparsely pubescent to glabrous.
v. Leaves 15–25 cm long, 8–15 cm wide; petiole 20–30 mm long; pedicel 6–10 mm long; style 3–4 mm long .... 14. *P. leptopedicellata*
vv. Leaves 5–13 cm long, 2–5 cm wide; petiole 4–17 mm long; pedicel 2–5 mm long; style 1–1.5 mm long .... 21. *P. stipitata*
tt. Sepals and corolla lobes generally 5-merous.
w. Leaves crowded at ends of stout branches; flowers and fruits borne on branches 7 mm or more in diameter .... 7. *P. congestifolia*
ww. Leaves scattered along slender branches; flowers and fruits usually borne on branches less than 5 mm in diameter.
x. Petiole flattened above, broadly canaliculate; fruit usually with 1 seed .... 11. *P. engleri*
xx. Petiole nearly terete, narrowly canaliculate; fruit usually with 5 seeds.
y. Fruit mealy roughened, even when young .... 15. *P. lucentifolia*
yy. Fruit nearly smooth, slightly low-tuberculate .... 17. *P. pentasperma*

1. **Pouteria buenaventurensis** (Aubréville) Pilz, comb. nov.

Richardella buenaventurensis Aubréville, Adansonia, n.s., 7: 146. 1967. TYPE: Colombia, Departmento del Valle, Río Yurumanguí, *Cuatrecasas 15821* (US).

Tree to 30 m. *Leaves* with petioles 1–2 cm long; blades elliptic to elliptic-oblanceolate, coriaceous, rounded to obtuse and occasionally abruptly acuminate, 8–18(–20) cm long, 4.5–6(–11) cm wide, sparsely rufous pubescent, glabrate; primary lateral veins 8–12 pairs, the secondary and tertiary laterals prominent, irregular, often branched, much of the venation perpendicular to the previous series. *Flowers* 1–3 in the axils and at recently defoliated nodes; pedicels 3–4 mm long; sepals 5–6, ovate, 3–6 mm wide, the outer 2–2.5 mm long, the inner 4–5 mm long, densely sericeous except on the margins and the lower portion of the adaxial surface; corolla greenish white, glabrous, cylindric, 7–12 mm long, the lobes 5, rounded, about ½ as long as the tube; filaments 3 mm long, attached at the level of the sinuses or slightly below, the staminodes lanceolate, 2–2.5 mm long; ovary densely pubescent, (4–)5-loculed, the style 8–10 mm long. *Fruit* to 4 cm long, globose, mealy roughened, brown; seeds solitary, to 2.8 cm long, globose, the seed scar covering ½–⅔ of the seed surface.

This species occurs in Colombia and Panama.

Although the plants are morphologically very similar, it must be noted that the Colombian specimens are all from low elevations (Departmento del Valle), while the Panamanian material was collected at elevations of 350 to 1,000 m.

COLÓN: Santa Rita Ridge road, 14 km from Boyd-Roosevelt Highway, *Mori & Kallunki 4907* (MO). PANAMÁ: Cerro Jefe, *Dwyer 9495* (F, MO); *Gentry 4874, 6144* (both MO). N of Goofy Lake, *Folsom et al. 1959* (MO). 16–20 km above Panamerican Highway on road from El Llano to Cartí-Tupile, *Kennedy 2709* (MO). 9–20.7 km above Panamerican Highway on road from El Llano to Cartí, *Mori & Kallunki 4686, 5113, 5151* (all MO).

2. **Pouteria caimito** (Ruiz & Pavón) Radlkofer, Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 12: 333. 1882; Aubréville, Adansonia, n.s., 1: 154. 1961.

Achras caimito Ruiz & Pavón, Fl. Peruv. 3: 18, *pl. 240.* 1802. TYPE: Peru, *Ruiz & Pavón* (F, isotype).

Tree to 30 m. *Leaves* 5–24 cm long, 2–9 cm wide, obovate-oblanceolate to elliptic, acuminate, rarely acute; petioles 5–15 mm long. *Flowers* 1–5 per axil, subsessile to sessile; sepals 4(–5), 3–4.5 mm long; corolla 5–8 mm long, the lobes 4(–5), about as long as the tube; filaments attached near the middle of the tube; ovary 4(–6)-loculed. *Fruit* yellow to brown, fleshy, 5–10 cm long, 4–8 cm wide, 1–4-seeded; seed scar extending the entire length of the seed, 3–4 mm wide (Blackwell, 1968).

This species occurs in Peru and Brazil and through northern South America to Panama. It is occasionally cultivated.

COLÓN: Salud Hills, *Lao & Holdridge 192* (MO, tentative identification of sterile specimen). DARIÉN: Sambú River, *Pittier 5555* (F, US).

3. **Pouteria calistophylla** (Standley) Baehni, Candollea 9: 419. 1942.

Lucuma calistophylla Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 252. 1929. TYPE: Panama, *Cooper 481* (F, holotype; K, NY, US, isotypes).

Tree ca. 20 m tall. *Leaves* 10–22 cm long, 5–10 cm wide, obovate or elliptic-obovate, acuminate; primary lateral veins 15–22 pairs; petioles 1–3 cm long. *Flowers* imperfectly known; pedicel ca. 5 mm long; sepals 5, ca. 2 mm long; corolla 5-lobed; filaments attached at the level of the sinuses; ovary probably 2-loculed. *Fruit* unknown (Blackwell, 1968).

Known definitely only from the type collection.

BOCAS DEL TORO: Cricamola Valley, *Cooper 481* (F, K, NY, US).

4. **Pouteria campechiana** (H.B.K.) Baehni, Candollea 9: 398. 1942.

Lucuma campechiana H.B.K., Nov. Gen. Sp. Pl. 3: 240. 1819. TYPE: Mexico, near Campeche, *Humboldt & Bonpland* (photo F).
Richardia campechiana (H.B.K.) Pierre, Not. Bot. Sapot. 20. 1890; Aubréville, Adansonia, n.s., 1: 175. 1961.
Radlkoferella glabrifolia (Pittier) Aubréville, Mem. New York Bot. Gard. 23: 206. 1972.
Lucuma glabrifolia Pittier, Contr. U.S. Natl. Herb. 20: 481. 1922. TYPE: Panama, *Pittier 6542* (US, holotype; EAP, F, NY, isotypes).

Tree to 30 m. *Leaves* 10–35 cm long, 4–10 cm wide, elliptic to narrowly obovate, acuminate to rarely rounded; primary lateral veins 12–20 pairs; petioles 1–3 cm long. *Flowers* (1–)2–4(–9) per axil; pedicels 8–15 mm long; sepals (4–)5 (–6), 5–10(–12) mm long; corolla 7–14 mm long, the lobes (4–)5(–7), as long as the tube or somewhat shorter; filaments attached slightly below the level of the sinuses; ovary (4–)5(–10)-loculed. *Fruit* yellow at maturity, fleshy and edible, to 7 cm long, 7 cm wide, 1–4-seeded; seed scar extending the entire length of the seed, 1–2 cm broad (Blackwell, 1968).

This species ranges from Mexico to Amazonas, Brazil. It is widely cultivated and many collections represent introduced plants.

Aubréville (1961, 1972) placed plants of this species into two closely related genera as *Richardella campechiana* and *Radlkoferella glabrifolia*. The variability in the number of flower parts, particularly the number of sepals and ovary locules, as well as leaf size and shape, and fruit characteristics has resulted in the proposal of at least ten allied taxa. Segregation of this species into related species or even subspecies would be artificial until extensive monographic studies are undertaken.

CANAL ZONE: Ancón, *Piper 6027* (F, US). Barro Colorado Island, *Zetek 5562* (EAP, MO). COCLÉ: Penonomé, *Williams 56* (US). COLÓN: Donoso, *Holdridge 6202* (MO). DARIÉN: Casaya Island, *Duke 10374* (MO). Piñas, *Duke 10589* (MO). Pinogana, *Pittier 6542* (EAP, F, NY, US). 2 mi E of Santa Fé, *Tyson et al. 4839* (MO). LOS SANTOS: Punta Mala, *Croat 9751* (MO). 16 mi S of Macaracas at Quebrada Bejuco, *Tyson et al. 3092* (MO). PANAMÁ: Trapiche Island, *Allen 2609, 2627* (both EAP, F); *Miller 1875, 1902* (both US). Chepillo Island, *Duke 10320* (MO). Saboga Island, *Duke 10343* (MO). Espiritu Santo Island, *Duke 10454* (MO). San José Island, *Erlanson 201, 235* (both US), *396* (EAP, US); *Johnston 526, 733, 1171* (all MO, US); *Miller 1928* (US). Río Pasiga, *Gentry 2310* (MO). Chichebre, Chepo, *Holdridge 6497* (MO). Pacheca Island, *Tyson et al. 5601, 5604* (both MO). VERAGUAS: Bahía Honda, Pueblo Nuevo, *Barclay 2827* (MO).

5. **Pouteria carabobensis** Pittier, Contr. Fl. Venez. 12. 1921. TYPE: Venezuela, hills of Guaremales, road from Puerto Cabello to San Felipe, *Pittier 8921* (US, holotype, photo MO; NY, isotype).

Tree to 25 m. *Leaves* with petioles 15–25 mm long; blades elliptic to elliptic-obovate, thin to firm, obtuse to acute, often abruptly acuminate, 12–22 cm long, 4–10 cm wide, very sparsely gray pubescent to glabrous; primary lateral veins 11–13 pairs, thin, the secondary laterals curved, oblique to the primary ones, those near the margin straighter and nearly perpendicular, the tertiary laterals very fine, anastomosing. *Flowers* 4–7 in the axils and at recently defoliated nodes; pedicels 3–8 mm long; sepals 4, ovate, 4 mm long, 4–5 mm wide, the outer ones pubescent on the abaxial surface, the inner ones and adaxial surfaces glabrous; corolla papillose, glabrous, 7–13 mm long, the lobes 4–5(–6), ovate, nearly equal to much shorter than the tube; filaments 1–2 mm long, attached at the level of the sinuses, the staminodes broadly lanceolate, 1.5–3 mm long; ovary pale pilose, 4-loculed, the style glabrous, 5–6 mm long. *Fruit* reputedly edible, otherwise unknown.

This species occurs in Venezuela and Panama.

Plants of this species have highly variable flowers. I have seen only flowers with 4 sepals, but the corollas may be 4–6-merous on the same branch.

DARIÉN: Río Tuquese, at middle Tuquesa Mining Company camp called Charco Peje, riverside, *Mori 7101* (MO).

6. **Pouteria chiricana** (Standley) Baehni, Candollea 9: 420. 1942.

Lucuma chiricana Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 251. 1929. TYPE: Panama, *Cooper & Slater 254* (F, holotype; NY, US, isotypes).

Tree to 30 m. *Leaves* 8–16 cm long, 2.5–6 cm wide, elliptic to oblong, acuminate; petioles 6–17 mm long. *Flowers* subsessile in the axils; sepals 5, 2.2–2.6 mm long; corolla 3–3.2 mm long, the lobes 5, about twice as long as the tube; ovary 4-loculed. *Fruit* fleshy, 3–3.5 cm long, 2–2.5 cm wide, 1-seeded; seed scar extending the length of the seed, ca. 8 mm wide (Blackwell, 1968).

This species occurs in Costa Rica and Panama.

Flowers with stamens have not been collected for *Pouteria chiricana*. Other Central American *Pouteria* known to possess heteromorphic flowers are *P. amydalina, P. durlandii,* and *P. stipitata*.

BOCAS DEL TORO: Almirante region, *Cooper 445* (F, NY), *457* (EAP, F, NY). CHIRIQUÍ: Progreso, *Cooper & Slater 230, 254* (both F, NY, US). Burica Peninsula, 9 mi S of Puerto Armuelles, *Croat 22107* (MO, NY).

7. **Pouteria congestifolia** Pilz.[3] TYPE: Panama, *Allen 3426* (MO, holotype; EAP, F, isotypes).

Tree 30 m tall. *Leaves* crowded at the ends of stout branches; petioles 2–3 cm long; blades oblanceolate, firm, 15–20 cm long, to 5 cm wide, mucronate to shallowly emarginate, sparsely pilose; primary lateral veins 15–20 pairs, the secondary ones somewhat sinuous, generally perpendicular to the primary laterals, the tertiary ones highly reticulate, nearly as prominent as the secondaries. *Flowers* 2–4 in the axils or at recently defoliated nodes; pedicels 4–10 mm long, rufous pubescent; sepals 5, ovate, 3–4 mm long, 2.5–3 mm wide, densely rufous sericeous externally except for the margin of the inner sepals, the adaxial surface of all sepals glabrous; corolla green, 4–5 mm long, the 5 lobes ciliolate, sparsely pubescent, about as long as the tube; filaments 1.5–2 mm long, attached near base of the tube, the staminodes lanceolate, 0.7 mm long; ovary 1–1.5 mm high, densely rufous pilose, 4–5-loculed, the style 1.5 mm tall, 5-lobed. *Fruit* unknown.

Known only from two collections. They are curious specimens that do not seem to be closely related to any species of my acquaintance. The combination of a 5-merous flower with filaments inserted near the base of the corolla tube and with well-developed staminodes is not frequently observed in American Sapo-

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[3] *Pouteria congestifolia* Pilz, sp. nov. *Arbor* 25 m alta. *Folia* ad ramulorum apicem dense congesta; petioli 2–3 cm longi; laminae oblanceolata, firmae, 15–20 cm longa, 4–5 cm lata, apice mucronata vel emarginata; costae 15–20 jugatae. *Flores* 2–4 ad axillam foliorum persistentium vel delapsorum fasciculati; pedicelli rufo-pubescentes, 4–10 mm longi; sepala 5, ovata, 3–4 mm longa, 2.5–3 mm lata, dorso rufo-sericeo, intus glabro; corolla 4–5 mm longa; lobi 5, ciliolati, tubo aequilongi; filamenta 1.5–2 mm longa, fere ad basin tubi affixa; staminodia lanceolata, 0.7 mm longa; ovarium 1–1.5 mm altus, dense pilosum, 4–5-loculare, cum stylo 1.5 mm longum. *Bacca* ignota.

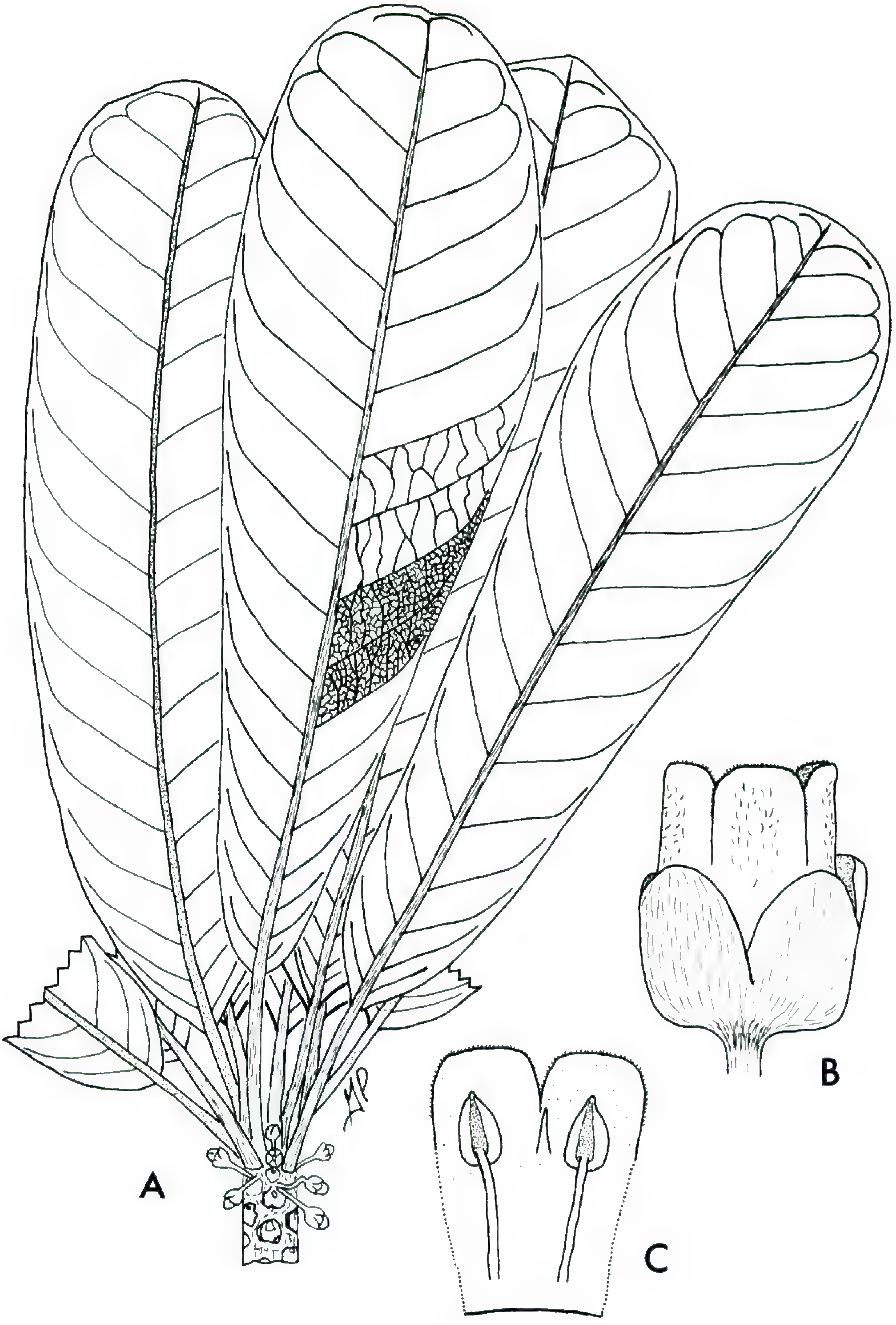

FIGURE 1. *Pouteria congestifolia* Pilz.—A. Habit (×7/10).—B. Flower (×7).—C. Corolla fragment (×7). [After *Allen 3426* (MO).]

taceae. Further generic speculation awaits the collection of fruits from this species.

The epithet *congestifolia* draws attention to the manner in which the leaves are crowded at the ends of stout branches.

CHIRIQUÍ: East of the Fortuna dam site, *Mendoza 370* (MO). COCLÉ: El Valle de Antón, 1000 m, *Allen 3426* (EAP, F, MO).

8. **Pouteria cooperi** Cronquist, Lloydia 9: 291. 1946. TYPE: Panama, *Cooper 499* (NY, holotype; EAP, F, US, isotypes).

Calocarpum cooperi (Cronquist) Lundell, Wrightia 5: 252. 1976.

Tree ca. 15 m tall. *Leaves* 8–17 cm long, 3–7 cm wide, elliptic or narrowly obovate, acuminate; primary lateral veins 8–13 pairs; petioles 1–3 cm long. *Flowers* subsessile; calyx of 10 or more thick, fleshy, broad sepals to 5 mm long; other flower parts unknown. *Fruit* reputedly woody (Blackwell, 1968).

This species is known only from the type collection.

BOCAS DEL TORO: Almirante region, Cricamola Valley, *Cooper 499* (EAP, F, NY, US).

9. **Pouteria dominigensis** (Gaertner f.) Baehni var. **dominigensis**, Lloydia 9: 278. 1946.

Lucuma dominigense Gaertner f., Fruct. 3: 131. 1807. TYPE: Haiti, *Poiteau*, not seen.
Radlkoferella domingensis (Gaertner f.) Pierre, Not. Bot. Sapot. 21. 1890; Aubréville, Adansonia, n.s., 1: 185. 1961.

Tree to 10 m. *Leaves* 4–13 cm long, 2–6 cm wide, obovate-oblanceolate, rounded, rarely acute; primary lateral veins 10–20 pairs; petioles 1–1.5 cm long. *Flowers* usually several per axil; pedicels 3–8 mm long; sepals 4, 4–9 mm long; corolla 8–16 mm long, the lobes (5–)6, about as long as the tube; filaments attached at the level of the sinuses; ovary (5–)6(–8)-loculed. *Fruit* yellow, fleshy, 2–5 cm long, 3–6 cm wide, 1–several-seeded; seed scar variable in length, 3–10 mm broad (Blackwell, 1968).

This species occurs in West Indies and southern Florida. It is cultivated in the Canal Zone.

CANAL ZONE: Without locality, *Johansen 36* (F, NY, US). Ancón, *Mell s.n.* (F, NY). Balboa, *Standley 26894* (F, MO, US), *30859* (F, US).

10. **Pouteria durlandii** (Standley) Baehni, Candollea 9: 422. 1942.

Lucuma durlandii Standley, Trop. Woods 4: 5. 1925. TYPE: Guatemala, Departmento Petén, El Paso, *Durland s.n.* (US, holotype; F, isotype).
Peteniodendron durlandii (Standley) Lundell, Wrightia 5: 254. 1975.
Paralabatia durlandii (Standley) Aubréville, Adansonia, n.s., 3: 21. 1963.

Tree to 25 m. *Leaves* with petioles 1–3 cm long; blades obovate to oblanceolate, firm, obtuse to abruptly acuminate, 10–25 cm long, 4–9 cm wide, essentially glabrous above, pale pubescent beneath, glabrate; primary lateral veins 8–13 pairs, the secondary and tertiary ones equally prominent with raised veins be-

neath. *Flowers* 1–3 in the axils or at recently defoliated nodes, often heteromorphic and unisexual, the pistillate flowers generally smaller than the staminate ones; pedicels 1–2 mm long, densely rufous pubescent; sepals 5, ovate, 2.5–4 mm long, 2–2.5 mm wide, sparsely to densely rufous pubescent; corolla greenish white, glabrous, 3–5.5 mm long, the lobes 5, ovate, equal in length to twice as long as the tube; filaments 0.5–1.5 mm long, attached at the level of the sinuses, the staminodes petaloid to lanceolate, 0.5–2 mm long; ovary densely rufous pubescent, 2(–5)-loculed, the style 0.8–1.5 mm long. *Fruit* yellow, subglobose, densely rufous pubescent, glabrate, to 2.5 cm long; seeds 1–3, ovoid to subglobose, to 2 cm long, the seed scar extending nearly the entire length of the seed, 4–11 mm broad, covering ⅓–½ of the seed.

This species occurs in Mexico, Guatemala, Belize, Honduras, Costa Rica, and Panama.

Peteniodendron Lundell (1975) is distinguished by its heteromorphic unisexual flower, 2–3-loculate ovary, pubescent fruits, and large seed scars. None of the above characteristics are unique to *Peteniodendron* and within the highly reticulated Poutereae *Peteniodendron* does not, at this time, deserve generic recognition. Other Central American *Pouteria* known to possess heteromorphic unisexual flowers are *P. amydalina, P. chiricana,* and *P. stipitata.*

Only young fruiting specimens have been collected in Panama, and their identity is problematic. Panamanian material differs from typical *Pouteria durlandii* in generally having 5-loculed ovaries, although ovaries with 2–5 locules were observed on the same branch.

DARIÉN: Without locality, *Duke 8357* (MO). Pirre, *Duke & Bristan 248* (MO).

11. **Pouteria engleri** Eyma, Recueil Trav. Bot. Néerl. 33: 178. 1936. TYPE: French Guiana, *Mélinon s.n.* (P, holotype; K, isotype).

Nemaluma engleri (Eyma) Aubréville & Pellegrin, Adansonia, n.s., 1: 31. 1961.

Tree to 20 m. *Leaves* with petioles 10–15(–25) mm long; blades obovate to elliptic-ovate, firm, rounded, mucronate, 6–15(–20) cm long, 3–8(–13) cm wide, very sparsely pale pubescent, glabrate; primary lateral veins 7–11 pairs, distinct, the secondary and tertiary ones obscure above, evident beneath, sinuous, areoles incomplete to lacking. *Flowers* 1–10(–20) in the axils of the leaves; pedicels 4–7 mm long, sparsely rufous pubescent; sepals 5, ovate, 2–2.2 mm long, 2 mm wide, sparsely rufous pubescent, glabrate; corolla greenish white, glabrous, 3.5–4 mm long, the lobes 5, ovate, about as long as the tube; filaments 1 mm long, attached near the middle or base of the tube, the staminodes rare, variable in number, deltoid, minute; ovary pale pubescent, 4–5-loculed, the style 2 mm long. *Fruit* ellipsoidal, 18–23 mm long, smooth, glabrous; seeds 1–5, ovoid, laterally compressed, 14–18 mm long, the seed scar linear, extending the entire length of the seed, 2.5 mm wide.

This species occurs in Surinam, Guyana, French Guiana, and Panama.

COLÓN: María Chiquita, *Holdridge 6524* (MO). PANAMÁ: El Llano to Cartí, *Correa et al. 1838* (MO, tentative identification of a badly parasitized specimen).

12. **Pouteria euryphylla** (Standley) Baehni, Candollea 9: 249. 1942.

Lucuma euryphylla Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 252. 1929. TYPE: Panama, *Cooper 611* (F, holotype; NY, isotype).

Tree ca. 15 m. *Leaves* 10–22 cm long, 4–12 cm wide, elliptic or obovate-elliptic, acuminate; primary lateral veins 9–13 pairs; petioles 1.5–6 cm long. *Flowers* few per axil; pedicels 4–5 mm long; sepals 4, ca. 3.5 mm long; corolla 3.7–4.5 mm long, the lobes 4(–5), about as long as the tube; filaments attached at about the middle of the tube; ovary 4-loculed. *Fruit* unknown (Blackwell, 1968).

Known only from the type collection. Most likely related to four species from Brazil and northern South America that are placed by Aubréville in *Pseudolabatia*.

BOCAS DEL TORO: Almirante region, Buena Vista Camp, *Cooper 611* (F, NY).

13. **Pouteria fossicola** Cronquist, Lloydia 9: 289. 1946. TYPE: Panama, Canal Zone, Barro Colorado Island, north shore near Pearson terminal, *Salvoza 999* (A, not seen).

Calocarpum fossicolum (Cronquist) Lundell, Wrightia 5: 252. 1976.
C. borucanum Standley & L. O. Williams, herbarium name, never validly published.

Tree to 30 m. *Leaves* 8–30 cm long, 4–13 cm wide, obovate, short-acuminate to obtuse; primary lateral veins 12–20 pairs; petioles 1–4.5 cm long. *Flowers* 1–5 in the axils of the leaves or at recently defoliated nodes; pedicels 4–6 mm long; sepals (6–)8(–9), spirally arranged, to 7 mm long; corolla white, densely pubescent except for the margins of the lobes and the base of the tube, cylindric, 9–11 mm long, the tube comprising ¾ of the total length, the lobes 5, ovate; filaments attached at the level of the sinuses or slightly below, 1–1.5 mm long, the staminodes lanceolate, 1–1.2 mm long; ovary 5-loculed. *Fruit* yellow green to grayish white, fleshy, 8–15 cm long, 4–9 cm wide, 1(–2)-seeded; seed scar extending the entire length of the seed, 3–4 cm broad (Blackwell, 1968).

This species occurs in Panama and southeastern Costa Rica.

As presently circumscribed, this species, once known only from Barro Colorado Island (Blackwell, 1968), extends to Puntarenas, Costa Rica, *Allen 5753* and *6636* (both EAP).

CANAL ZONE: Barro Colorado Island, *Bangham 583* (F); *Zetek 3870* (F, MO). COCLÉ: El Valle de Antón, *Lao 278* (MO). El Valle de Antón, 600 m, cultivated tree, *Nee & Dwyer 9218* (MO). COLÓN: Santa Rita lumber road, 9.4 km from Transisthmian Highway, *Dressler 3811* (MO).

14. **Pouteria leptopedicellata** Pilz.[4] TYPE: Panama, *Mori & Kallunki 5064* (MO).

Tree 20 m tall. *Leaves* with petioles 2–3 cm long; blades oblanceolate, firm, 15–25 cm long, 8–15 cm wide, rounded to abruptly acuminate, very sparsely

[4] *Pouteria leptopedicellata* Pilz, sp. nov. *Arbor* 20 m alta. *Folia* cum petioli 2–3 cm longi; laminae oblanceolata, firmae, 15–25 cm longa, 8–15 cm lata, apice rotundata vel abrupte acuminata, glabriuscula; costae 9–12 jugatae. *Flores* 10–20 ad axillam foliorum persistentium vel delapsorum fasciculati; pedicelli glabri, 6–10 mm longi; sepala 4, ovata, 2–3 mm longa, glabra; corolla 4 mm longa; lobi 4; tubo 2–3-plo longiores; filamenta 1–1.5 mm longa, medio tubo affixa; staminodia spathulata, 0.7 mm longa; ovarium dense rufo-pilosum, 4-loculare, cum stylo 3–4 mm longum. *Bacca* ignota.

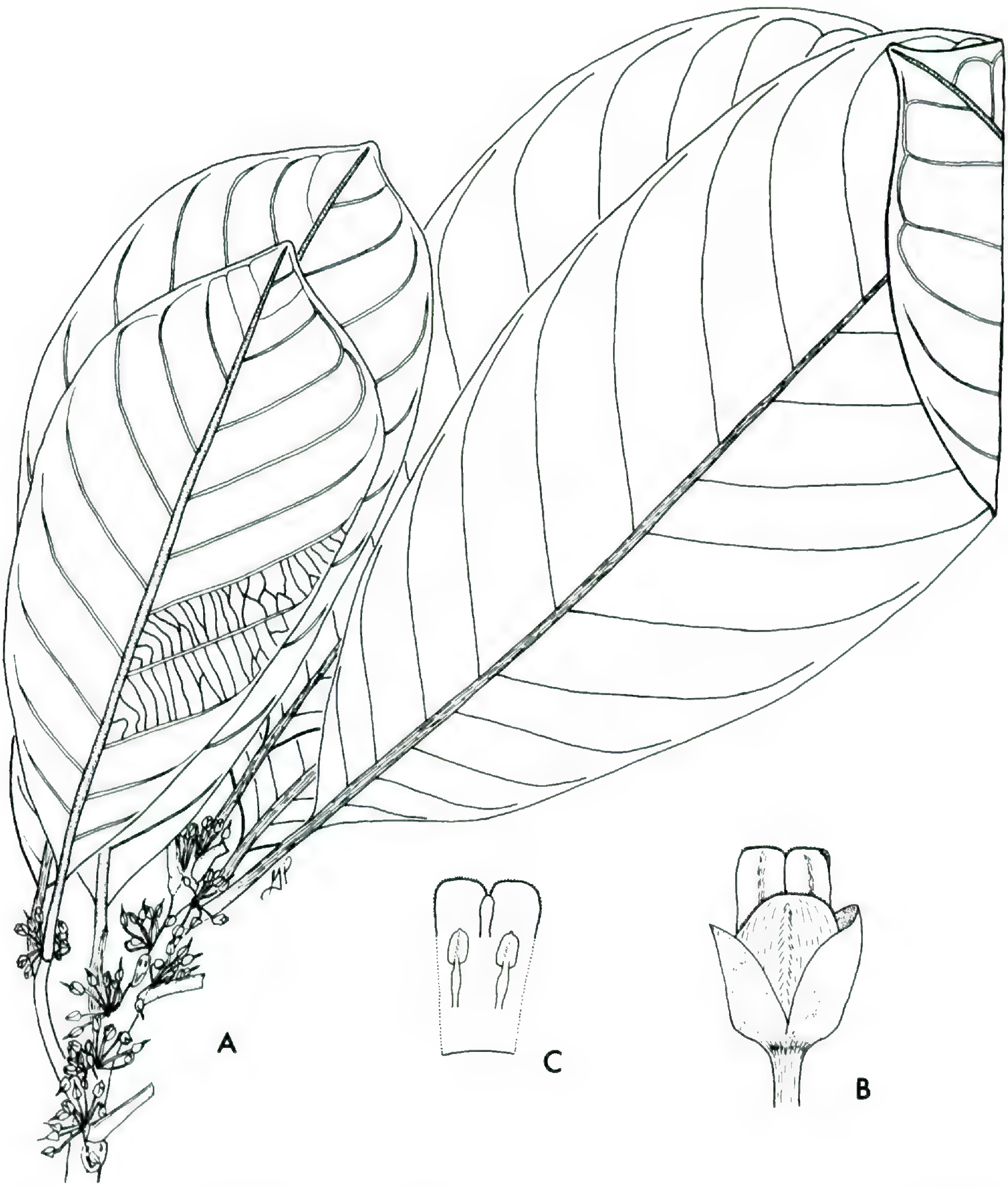

FIGURE 2. *Pouteria leptopedicellata* Pilz.—A. Habit (×½).—B. Flower (×5).—C. Corolla fragment (×5). [After *Mori & Kallunki 5064* (MO).]

pubescent, glabrate; primary lateral veins 9–12 pairs, the secondary and tertiary ones irregularly branching, generally perpendicular to those of the previous series. *Flowers* 10–20 in the axils or at recently defoliated nodes; pedicels 6–10 mm long, glabrous; sepals 4, ovate, 2–3 mm long, glabrous except for scattered hairs at the base of the adaxial surface; corolla 4 mm long, the 4 lobes smooth to minutely ciliolate, ⅓–½ as long as the tube; filaments 1–1.5 mm long, attached near the middle of the tube or below, the staminodes spatulate, 0.7 mm long; ovary densely rufous pilose, 4-loculed, the style 3–4 mm tall. *Fruit* unknown.

Pouteria leptopedicellata is closely related to *P. euryphylla* from Panama and *P. quicheana* from Guatemala; all are known only from flowering specimens of the type collections. *Pouteria euryphylla* is generally finely pale sericeous-strigose, while *P. leptopedicellata* possesses essentially glabrous sepals, pedicels, and leaves. In addition, *Pouteria leptopedicellata* possesses more flowers per node on much longer pedicels.

COLÓN: Santa Rita Ridge road 10.2 km from Boyd-Roosevelt Highway, 350 m, *Mori & Kallunki 5064* (MO).

15. **Pouteria lucentifolia** (Standley) Baehni, Candollea 9: 424. 1942.

Lucuma lucentifolia Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 251. 1929. TYPE: Costa Rica, Talamanca Valley, *Cooper 13* (F, holotype; EAP, US, isotypes).

Tree to 11 m. *Leaves* 7–25 cm long, 3–10 cm wide, elliptic-obovate, acuminate to rarely obtuse; primary lateral veins 8–14 pairs; petioles 8–24 mm long. *Flowers* 3–7 at recently defoliated nodes; pedicels 6–8 mm long, sparsely pubescent; sepals 5, ovate, fringed ciliolate, 3–3.5 mm long, 3 mm wide, sparsely pubescent; corolla greenish white, glabrous, campanulate, 5–5.5 mm long, the lobes 5, slightly shorter than the tube; filaments 1–1.5 mm long, attached near the base of the tube, the staminodes lanceolate, 0.7 mm long, occasionally absent; ovary densely rufous pubescent at the base, otherwise glabrous, 5-loculed, the style 1.5–2 mm long. *Fruit* brown, mealy roughened even when young, fleshy, 4–6 cm long, 4–6 cm wide, 5-seeded; seed scar extending the entire length of the seed, 1.5–2 mm broad (Blackwell, 1968).

This species occurs in Honduras, Costa Rica, and Panama.

The flowers of *Pouteria lucentifolia* are described here for the first time. Only a single flowering collection (*Mori 6243*) has been made, and the complete absence of staminodes in some flowers warrants further study. *Pouteria lucentifolia* is closely related to *P. pentasperma* and shares many attributes with *P. engleri*, placed by Aubréville in the monotypic *Nemaluma*.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 591* (F). Almirante, *Lao & Gentry 449* (F, MO). COCLÉ: N of El Valle de Antón, *Allen 3642* (F, K, MO, NY, US); *Lao 288* (MO). Base of Cerro Pilon above El Valle, *Gentry 3672* (MO). PANAMÁ: Below Cerro Campana, *Croat 14235* (MO). VERAGUAS: Cerro Tute, *Lao & Gentry 527* (MO, NY); *Mori 6243* (MO, NY). NW of Santa Fé, 1 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 4814, 4883* (both MO).

16. **Pouteria neglecta** Cronquist, Lloydia 9: 286. 1946. TYPE: Belize, primary forest, Temash River, *Schipp 1354* (MICH, holotype, not seen; F, MO, NY, isotypes).

Tree to 20 m. *Leaves* with petioles 1–4 cm long; blades broadly oblanceolate to obovate, firm, acuminate, 10–50 cm long, 4–16 cm wide, glabrous above, rufous hirsute particularly along the midrib and main veins beneath, glabrate; primary lateral veins 20–35 pairs, veins prominent and conspicuous beneath, the secondary laterals essentially perpendicular to and connecting the primary laterals, distinctly more prominent than the close reticulum. *Flowers* clustered at recently defoliated nodes, subsessile; sepals 4, the outer suborbicular and enclosing the obovate inner sepals, 7–9 mm long, pubescent; corolla greenish white, glabrous,

cylindric, 6–9 mm long, the lobes 4, ovate, ⅓ to equal the length of the tube; filaments 3–5 mm long, attached near the base of the tube, the staminodes linear-cylindric to subulate, 1.5–3 mm long; ovary rufous pubescent, 4-loculed, the style 2.5–8 mm long. *Fruit* to 5 cm long, subglobose, gall-like, covered with 1–2 cm long hairy processes; seeds 1–2, ovoid to subspherical, 2–3 cm long, 1.3–1.6 cm wide, the seed scar covering ca. ½ the seed surface, extending the entire length of the seed, 8 mm broad.

This species ranges from Guatemala to Panama and perhaps Peru.

The circumscription of *Pouteria neglecta* has been enlarged from that originally proposed by Cronquist in order to accommodate Panamanian material, particularly collections from Darién. In many respects Panamanian material approaches the Peruvian *P. wurdackii* Aubréville (Adansonia 5: 201. 1965), with its larger corolla, proportionally longer tube and longer style. As more material is collected, it may be possible to determine the variability of the Peruvian material and to decide whether it is conspecific to *P. neglecta*.

CANAL ZONE: Pipeline road, *Croat 16619* (MO, NY); *Lao et al. 11* (F, MO); *Spellman et al. 533* (MO). DARIÉN: Quebrada Aguacate, *Bristan 1208* (MO). Cerro Pirre, *Bristan 1225* (MO). Río Tucutí near Tucutí, *Duke 5253* (MO). Río Pirre, Dos Bocas, *Foster & Augspurger 2841* (MO). Cerro Pirre base-camp on Río Parasenico, *Gentry 4770, Gentry & Clewell 7060* (both MO).

17. **Pouteria pentasperma** (Standley) Baehni, Candollea 9: 353. 1942.

Lucuma pentasperma Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 251. 1929. TYPE: Panama, *Cooper 369* (F, holotype; K, NY, US, isotypes).

Tree to 15 m. *Leaves* with petioles 15–35 mm long; blades elliptic to obovate, firm, acute to obtuse, often short-acuminate, 10–25 cm long, 4–8 cm wide, very sparsely rufous pubescent, soon glabrate; primary lateral veins 12–18 pairs, the secondary and tertiary ones irregularly anastomosing. *Flowers* 4–6 in the axils and at recently defoliated nodes; pedicels 5–7 mm long; sepals (4–)5, ovate, 2 mm long, 2 mm wide, pale pubescent on the abaxial surface, particularly so near the base, the margins thin, undulate; other flower parts unknown. *Fruit* brown to golden brown, to 5 cm long, subglobose, smooth to low-tuberculate; seeds 5, 17–25 mm long, 9–12 mm wide, 4–7 mm thick, the seed scar 1.5–2 mm broad, extending 4/5 to the entire length of the seed.

This species is known only from Panama.

Cronquist (1946) and Blackwell (1968) considered *Pouteria pentasperma* to be a taxonomic synonym of *P. lucentifolia*. The leaves and seeds look quite similar, but the fruit of *P. pentasperma* is smooth at maturity while that of *P. lucentifolia* is mealy roughened even when very young. The nature of the fruit of these taxa is sufficiently constant to warrant specific separation, at least until the flowers of *P. pentasperma* are known.

BOCAS DEL TORO: Almirante region, *Cooper 369* (F, K, NY, US). DARIÉN: Río Congo, *Holdridge 6279* (MO). Santa Fé, Cuipo Forest Site 2, *Duke 14295* (MO). 3 mi N of Santa Fé, *Tyson et al. 4630* (MO). 2 mi E of Santa Fé, *Tyson et al. 4839* (MO). PROVINCE UNKNOWN: Mixed label, *Duke 12552* (MO).

18. **Pouteria sambuensis** (Pittier) Baehni, Candollea 9: 250. 1942.

Lucuma sambuensis Pittier, Contr. U.S. Natl. Herb. 18: 167. 1916. TYPE: Panama, *Pittier 5621* (US, holotype; F, isotype).

Tree 10 m tall. *Leaves* 18–25 cm long, 5–9 cm wide, oblanceolate to obovate, acuminate; primary lateral veins 13–15 pairs; petioles 1–1.5 cm long. *Flowers* subsessile; sepals 4; other flower parts unknown. *Fruit* fleshy, 5 cm long, 4 cm wide, densely rusty puberulous, several-seeded; seed scar unknown (Blackwell, 1968).

Known only from the type collection.

DARIÉN: Foothills of the Garagara Mts., Sambu Valley, *Pittier 5621* (F, US).

19. **Pouteria sapota** (Jacq.) Moore & Stearn, Taxon 16: 383. 1967.

Sideroxylum sapota Jacq., Enum. Pl. Carib. 15. 1760. TYPE: *pl. 218,* H. Sloane, The Natural History of Jamaica. Vol. 2. 1725.
Calocarpum sapota (Jacq.) Merrill, Enum. Philipp. Fl. Pl. 3: 284. 1923.

Tree to 30 m. *Leaves* 10–60 cm long, 4–15 cm wide, oblanceolate to obovate, usually acuminate; primary lateral veins 20–50 pairs; petioles 1–4.5 cm long. *Flowers* clustered at recently defoliated nodes, subsessile; sepals 8–12, 2–6 mm long; corolla 6–10 mm long, the lobes (4–)5, about as long as the tube; filaments attached at the level of the sinuses; ovary 5-loculed. *Fruit* brown, fleshy, 8–20 cm long, 5–12 cm wide, 1-seeded; seed scar extending the entire length of the seed, 2–2.5 cm broad (Blackwell, 1968).

This species ranges from Mexico and the West Indies to northern South America. It is widely cultivated, and many collections represent introduced plants.

CANAL ZONE: NW edge of Gamboa, *Mori & Kallunki 4723* (MO). W of Gamboa, *Nee 9474* (MO). ½–1 mi below Chilibre, *Seibert 1517* (MO, US). Balboa, *Standley 26080* (US). CHIRIQUÍ: Santa Clara region, 27 km NW of El Hato del Volcán, *Mori & Bolten 7214* (MO). Banks of Río Tabasará, *Woodson et al. 441* (MO). COCLÉ: Olá, *Pittier 5089* (NY, US). DARIÉN: El Real, *Correa & Lazor 1569* (MO). HERRERA: Las Minas to Pesé, *Duke 12307* (MO). PANAMÁ: Arraiján, *Lao 108* (MO). Laguna de Portala, Chepo, *Pittier 4628* (US). Tabago Island, *Standley 27916* (US). SAN BLAS: Between Río Diablo and Río Acuati, *Duke 14904* (MO). Ailigandí, *Dwyer 6849* (MO). Mainland opposite Playon Chico, *Gentry 6395* (MO). Mainland opposite Ailigandí, from mouth of Ailigandí River to 2.5 mi inland, *Lewis et al. 163* (MO, UC, US).

20. **Pouteria sclerocarpa** (Pittier) Cronquist, Lloydia 9: 287. 1946.

Lucuma sclerocarpa Pittier, Contr. U.S. Natl. Herb. 18: 166. 1916. TYPE: Panama, *Pittier 4357* (US, holotype; F, MO, NY, isotypes).
Calocarpum sclerocarpum (Pittier) Lundell, Wrightia 5: 253. 1976.

Tree 25 m. *Leaves* 10–25 cm long, 4–8 cm wide, elliptic-obovate, acuminate; primary lateral veins 13–20 pairs; petioles 1–2.2 cm long. *Flowers* several per axil, subsessile; sepals 6–7, to 6.5 mm long; corolla 6–8 mm long, the lobes 5, about ½ as long as the tube; filaments attached at the level of the sinuses; ovary 5-loculed. *Fruit* yellow, sclerous, 5–7.5 cm long, 3–4.5 cm wide, 1-seeded; seed scar extending the entire length of the seed, ca. 2 cm wide (Blackwell, 1968).

This species is known definitely only from the type collection. Two collections from Darién (*Duke 8593* and *Bristan 1294,* both MO) are only tentatively determined to be this species.

SAN BLAS: Plain of Sperdi, near Puerto Obaldía, *Pittier 4357* (F, MO, NY, US).

21. **Pouteria stipitata** Cronquist, Lloydia 9: 265. 1946. TYPE: Panama, *Zetek 4693* (F, holotype; EAP, MO, isotypes).

Tree to 20 m. *Leaves* 6–13 cm long, 2–4.5 cm wide, elliptic to narrowly obovate, acuminate; primary lateral veins 7–11 pairs; petioles 4–17 mm long. *Flowers* clustered at the defoliated nodes, occasionally heteromorphic and unisexual; pedicels 3–8 mm long; sepals 4–5, 2–2.5 mm long; corolla 2.3–3.2 mm long, the lobes 4, ca. ½ as long as the tube; filaments attached at the middle of the corolla tube; ovary 4-loculed. *Fruit* yellow, flesh scanty, 2–3.5 cm long, 1.5–2 cm wide, constricted to a stipe ca. 7 mm long and 3 mm thick, 1-seeded; seed scar extending the entire length of the seed, 8–10 mm broad (Blackwell, 1968).

This species is known only from Panama. Most collections are from Barro Colorado Island and the Perlas Archipelago.

Pouteria stipitata is most likely related to four species from Brazil and northern South America that are placed by Aubréville in *Pseudolabatia*.

CANAL ZONE: Barro Colorado Island, *Croat 10291* (F, MO, NY), *10293* (F, MO, UC); *Shattuck 1125* (F, MO); *Zetek 4693* (EAP, F, MO). DARIÉN: Chepigana, *Terry & Terry 1504* (F, MO), only a tentative identification. PANAMÁ: San José Island, *Erlanson 324* (US); *Johnston 634* (MO, NY, US). El Llano to Cartí-Tupile road, 12 mi above Panamerican Highway, *Liesner 1220* (MO).

22. **Pouteria stylosa** (Pierre) Dubard in Lecomte, Not. Syst. 1: 381. 1911.

Guapeba stylosa Pierre, Not. Bot. Sapot. 42. 1891. TYPE: Panama, *Sutton-Hayes 67* (not seen). *Neolabatia stylosa* (Pierre) Aubréville, Mem. New York Bot. Gard. 23: 203. 1972.

Tree to 7 m. *Leaves* 7–20 cm long, 2.5–7 cm wide, elliptic to narrowly obovate, acuminate; primary lateral veins 10–20 pairs; petioles 3–10 mm long. *Flowers* clustered in the axils or at recently defoliated nodes, sessile to subsessile; sepals 4, 2.5–4 mm long; corolla 2.5–4 mm long, the lobes 4, ½ as long as the tube; filaments attached near the base of the tube; ovary 4(–6)-loculed. *Fruit* woody, ca. 3 cm long, 3.5 cm wide, 2-seeded; seed scar nearly extending over the entire surface except for an elliptical area ca. 5 mm wide (Blackwell, 1968).

This species occurs in Panama, and perhaps from Honduras to Colombia.

BOCAS DEL TORO: Almirante region, Konkintoe, 10 mi above Holstein, *Cooper 509* (F). CANAL ZONE: W of Limón Bay, Gatún Locks and Gatún Lake, *Johnston 1820* (MO). Mamei Hill, *Pittier 3807* (F, NY, US). Hills near Gatún, *Standley 27193* (MO, US). Obispo, *Standley 31684* (US). PANAMÁ: El Cermeño, *Allen 2572* (F, NY); *Zetek 4804* (F, MO). Chiltepe, *Holdridge 6466* (MO). Vista Alegre, Río Aguacate, 2 mi beyond Arraiján, *Lao 589* (MO); *Zetek 5511* (EAP, F, MO, US).

23. **Pouteria subrotata** Cronquist, Lloydia 9: 277. 1946. TYPE: Panama, *Pittier 6548* (US).

Tree to 15 m. *Leaves* 10–23 cm long, 5–12 cm wide, obovate, acuminate; primary lateral veins 8–11 pairs; petioles 1.5–3 cm. *Flowers* several in the axils of the leaves and at recently defoliated nodes, subsessile; sepals 5, 1.7–2 mm long; corolla 3.5–3.8 mm long, the lobes 5, twice as long as the tube; filaments attached at the level of the sinuses; ovary 5-loculed. *Fruit* yellow green, turning red, 2–2.5 cm long, 1–1.3 cm wide, the flesh scant, 1-seeded; seed scar extending the entire length, 8–9 mm broad (Blackwell, 1968).

This species occurs in Panama and southeastern Costa Rica.

Pouteria subrotata is evidently related to species placed by Aubréville in *Richardella* Pierre.

COLÓN: East Ridge, *Duke 15265* (MO). DARIÉN: Río Ucurgantí, *Bristan 1122, 1177* (both MO). La Boca de Pirre, *Bristan 1273* (MO). 1–4 mi N of Pucro, *Duke 13003* (MO). Río Paya, *Duke & Kirkbride 14073* (MO, NY). Pinogana, *Pittier 6548* (US).

24. **Pouteria tarapotensis** (Eichl. ex Pierre) Baehni, Candollea 9: 273. 1942.

Lucuma tarapotensis Eichl. ex Pierre, Not. Bot. Sapot. 24. 1890. TYPE: Peru, near Tarapoto, *Spruce 4561* (F, K, NY, P, isotypes).
Franchetella tarapotensis (Eichl. ex Pierre) Pierre, Not. Bot. Sapot. 24. 1890; Aubréville, Adansonia, n.s., 1: 183. 1961.

Tree to 15 m. *Leaves* with petioles 15–25 mm long; blades elliptic, firm, narrowly acuminate, 13–18 cm long, 4–7 cm wide, densely pale sericeous beneath, sparsely pubescent above; primary lateral veins 9–14 pairs, not becoming crowded near the base, the secondary laterals rather irregular and sinuous, perpendicular to the primary series only near the margin. *Flowers* 12–20 in the axils or at recently defoliated nodes; pedicels 3–5 mm long at anthesis; sepals 5, ovate, 1 mm long, 1 mm wide, densely pubescent; corolla glabrous, 2–2.5 mm long, the lobes 5, ovate, rounded, fringed-ciliolate, as long as the tube; filaments 0.5 mm long, attached at the level of the sinuses, the staminodes triangular-lanceolate, often ciliolate, 0.7–1 mm long; ovary densely pubescent, 0.7 mm high, 1-loculed, the style 0.7 mm long. *Fruit* unknown in Panama, in Peru brown-pilose, oliviform, 20–25 mm long, 7–9 mm wide, 1-seeded; seed scar completely covering the compressed adaxial face.

This species occurs in Peru, Brazil, and Panama.

The identity of the specimen is problematic. Typical *Pouteria tarapotensis* differs from the Panamanian material described above in possessing generally shorter petioles, 5–7 mm long, smaller obovate leaves, 9–16 × 3–7 cm, fewer flowers per axil, 5–8, and much shorter pedicels, to 1 mm long. Fruits from Panama have not been collected, and when better known, these plants may prove to represent a distinct species.

PANAMÁ: 6 km above Panamerican Highway on road from El Llano to Cartí-Tupile, *Kennedy 1805* (MO).

25. **Pouteria unilocularis** (Donn. Smith) Baehni, Candollea 9: 273. 1942.

Sideroxylon uniloculare Donn. Smith, Bot. Gaz. (Crawfordsville) 35: 5. 1903. TYPE: Costa Rica, Tucurrique, Río de las Vueltas, *Tonduz 13358* (F, K, isotypes).
Franchetella unilocularis (Donn. Smith) Aubréville, Adansonia, n.s., 3: 21. 1963.

Tree to 20 m. *Leaves* with petioles 7–10 mm long; blades elliptic, firm, acuminate, 7–14(–20) cm long, 3–7(–9) cm wide, glabrous; primary lateral veins 12–14 pairs, the secondary and tertiary ones closely reticulate. *Flowers* 5–10 in the axils or at recently defoliated nodes; pedicels 3–7 mm long; sepals (4–)5(–6), ovate, 1.4–1.7 mm long, ca. 1 mm wide, sparsely rufous pubescent; corolla white, glabrous, 2.2–2.7 mm long, the lobes (4–)5, fringed-ciliolate, about twice as long as the tube; filaments to 0.5 mm long, attached at the level of the sinuses or slightly below, the staminodes triangular-lanceolate, often petaloid, 0.7–1 mm long; ovary sparsely pubescent, 1-loculed, the style 0.5 mm long. *Fruit* yellow, obovoid to subglobose, 1.5–2 cm long; seeds solitary, to 14 mm long, 8 mm wide, ellipsoidal, the seed scar extending the entire length of the seed, 3–5 mm wide.

This species occurs in Mexico, Belize, Guatemala, Honduras, Costa Rica, and Panama.

Pouteria unilocularis is evidently closely related to *P. tarapotensis*, but it can be readily distinguished by its essentially glabrous leaves.

CANAL ZONE: Barro Colorado Island, *Croat 10971, 17052* (both MO); *Croat 14874* (MO, NY); *Zetek 5148* (EAP, F, MO). CHIRIQUÍ: Gualaca to Fortuna dam site, NW of Los Planes de Hornito, *Croat 49844* (MO). DARIÉN: Río Ucurgantí, *Bristan 1184* (MO, NY).

11. SYNSEPALUM

Synsepalum (A. DC.) Daniell in Bell, Pharm. J. Trans. 11: 445. 1852. TYPE: *S. dulcificum* (Schum. & Thonn.) Daniell.

Shrubs or small trees lacking spines. *Leaves* alternate, exstipulate; blades firm, the lateral veins generally few. *Flowers* sessile or short-pedicellate; sepals 5, uniseriate, united for more than half their length; corolla lobes 5, lacking appendages; stamens epipetalous, the filaments attached at the level of the sinuses, the staminodes alternating with the stamens, petaloid; ovary 5-loculed. *Fruit* baccate; seeds solitary, the seed scar lateral, very broad, covering about half the seed, the endosperm absent, the cotyledons fleshy.

Synsepalum is a tropical African genus of about 8 species.

1. **Synsepalum dulcificum** (Schum. & Thonn.) Daniell in Bell, Pharm. J. Trans. 11: 445. 1852.

Bumelia dulcifica Schum. & Thonn. in Beskr. Guin. Pl. 130. 1827. TYPE: not seen.

Shrub or small tree to 3 m. *Leaves* with petioles 2–5 mm long; blades elliptic to obovate, firm, obtuse or mucronate (emarginate), 5–10 cm long, 2–5 cm wide, glabrescent; primary lateral veins 8–13 pairs, the secondary and tertiary ones irregularly anastomosing, raised above, obscure below. *Flowers* 1–5(–10) in the axils or at recently defoliated nodes; pedicels to 2 mm long, rufous tomentose; calyx 3–5 mm long, the 5 lobes short, triangular, rufous pubescent; corolla glabrous, 5–7 mm long, the 5 lobes entire, about as long as the tube; filaments attached at the level of the sinuses, the staminodes erose, ovate, 2 mm long; ovary pubescent, 5-loculed, the style 5–10 mm long. *Fruit* red purple at maturity, ovoid, 1.6–2 cm long; seeds solitary, ovoid, 1.2–1.5 cm long, the seed scar lateral, very broad, covering about half the seed and extending the entire length.

This species occurs in west and central Africa from Ghana, Benin, southern Nigeria, Cameroun, to Zaire. It is widely cultivated in the tropics.

The fruits of the "Miracle Berry," when eaten, have the peculiar property of making anything eaten within 2 or 3 hours afterwards taste sweet, even very acid substances like sour limes (Nigerian Trees 2: 363. 1964).

CANAL ZONE: Summit Gardens, *Gentry 4997* (MO); *Steyermark* (MO).

THE MEXICAN AND CENTRAL AMERICAN SPECIES OF *ADELOBOTRYS* (MELASTOMATACEAE)[1]

FRANK ALMEDA, JR.[2]

ABSTRACT

Adelobotrys, a neotropical genus comprising ca. 25 described species, is largely restricted to the Amazon basin and adjacent regions of South America. The Mexican and Central American species represent geographical fringe elements of the genus and show no close similarities to one another. *Adelobotrys panamensis* and *A. jefensis* are described as new and presented in the context of a regional revision with a key, descriptions, brief discussions, illustrations and citation of representative specimens.

Adelobotrys, comprising some 25 described species is one of five merianioid genera currently recorded from tropical regions north of the South American continent. Although centered in the Amazon basin, *Adelobotrys* ranges south to Bolivia, east to Surinam and north through Central America to southern Mexico and Jamaica. The genus has never been the subject of a comprehensive revision but information gleaned from descriptions of new species and regional floristic accounts indicates that *Adelobotrys* is typically a genus of lowland rainforest habitats. Some species grow at elevations as high as 1,000 meters and a few are apparently restricted to the lower elevation montane slopes which are frequently shrouded in mist because of their geographic position and exposure. In this paper I describe two new Panamanian species of local distribution which fall into the latter category. These novelties are described in the context of a regional treatment with a key and descriptions that will readily facilitate identification and comparison of the Mexican and Central American species.

The species considered here represent geographical fringe elements of the genus and for this reason it is not surprising that they show no close similarities to one another. Each appears to have closest affinities with a different group of South American species but a confident assessment of relationships must await critical study of the entire genus.

ADELOBOTRYS DC., Prodr. 3: 127. 1828

Erect shrubs, small trees to 3.5 m, scandent woody vines or hemiepiphytes adhering to tree trunks by adventitious roots. *Internodes* glabrous to variously pubescent, terete or ± compressed and 2-edged. *Leaves* opposite, decussate or distichous, those of a pair equal to slightly unequal, petiolate or subsessile, glabrous or variously beset with malpighiaceous trichomes. *Inflorescence* terminal

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or axillary, multiflowered and paniculate or conspicuously contracted and umbelliform. *Flowers* perigynous; hypanthium free from the ovary but fully enveloping it, cylindric to campanulate or commonly urceolate, terete and smooth or strongly costate in fruit. *Calyx tube* usually well developed and flangelike; calyx lobes broadly ovate to hemispheric or markedly depressed and evident as low, truncate undulations; calyx teeth conspicuous and exceeding the calyx lobes or obsolete. *Petals* 5, free and spreading, obovate, entire, and sometimes obliquely rounded apically. *Stamens* 10, isomorphic to anisomorphic, geniculate; filaments complanate and ± declined to one side of flower; anthers linear-subulate, often arcuate and terminated by a solitary pore, the connective not prolonged below the thecae but variously modified dorsally into simple and/or bifid spurs and appendages. *Ovary* superior, cylindric to ovoid, glabrous and 5-celled. *Style* usually glabrous and ± declinate; stigma truncate or punctiform. *Capsule* dry, leathery, loculicidal. *Seeds* narrowly linear-cuneate and winged to caudate at both ends or short-cuneate and conspicuously angled.

Various authors (Gleason, 1932; Macbride, 1941) have distinguished *Adelobotrys* from related genera by its scandent vining habit, vestiture of malpighiaceous hairs, and tailed or winged seeds. These features have served to distinguish species of *Adelobotrys* from prescribed geographic areas, but it would be misleading to invoke only this constellation of characters for a strict characterization of the genus. Some species, for example, attain arborescent dimensions, some are totally glabrous, and yet other species have short cuneiform seeds with no vestige of wings or caudiform ornamentations. Evaluation of generic limits in the tribe Merianieae is much needed and may ultimately lead to an amalgamation of genera that have conventionally been accorded generic status. In this study I recognize *Adelobotrys* as a distinct and useful taxon most readily distinguished from other Mexican and Central American Merianieae by the distinctive inflorescences of either panicled umbels or axillary umbelliform clusters and by the highly modified anther connective consisting of a short acute or bilobed basal spur and an elongate, bifid or simple, ascending dorsal appendage.

Key to the Species of *Adelobotrys* of Mexico and Central America

1a. Shrub or small tree, the young branches flattened and 2-edged; distal internodes, vegetative buds, immature hypanthia, and branchlets of the inflorescence glabrous; principal leaves acute to rarely obtuse basally; inflorescence a congested axillary umbel arising from short branchlets 5–8 mm long .... 1. *A. panamensis*

1b. Scandent vine or hemiepiphyte adhering to tree trunks by adventitious roots, the young branches terete; distal internodes, vegetative buds, immature hypanthia, and branchlets of the inflorescence beset with brown malpighiaceous hairs; principal leaves broadly rounded to cordate or auriculate basally; inflorescence a terminal panicle with the ultimate units consisting of solitary flowers or 2–6(–12)-flowered umbels.

  2a. Principal leaves prevailingly ovate, elliptic-ovate or subrotund, broadly rounded to cordate basally, (5.6–)7.5–22 cm long and 3–13.5 cm wide; petioles 1.0–3.5(–5.5) cm long; calyx lobes obsolete or consisting of poorly developed truncate undulations; calyx teeth obsolete, if present then mostly minute and inconspicuous or only slightly exceeding the calyx lobes .... 2. *A. adscendens*

  2b. Principal leaves prevailingly elliptic to elliptic-ovate, cordate-clasping to auriculate basally, (2.5–)3.0–4.6 cm long and 1.3–2.8 cm wide; petioles (0.1–)0.2–0.3 cm long; calyx lobes well developed, broadly deltoid to hemispheric; calyx teeth conspicuous and markedly exceeding the calyx lobes .... 3. *A. jefensis*

1. **Adelobotrys panamensis** Almeda, sp. nov.—FIG. 1.

Frutex vel arbuscula ad 2–3.5 m altus, ramis, petiolis, foliis, et pedunculis omnino glabris. Folia in dimensionibus paulo inaequalia in forma isomorphica. Petioli (0.7–)1.5–4.0 cm; lamina 9–26 × 5.5–12.5 cm elliptica vel elliptico-lanceolata, apice acuminato vel cuspidato basi acuta vel obtusa, 5-plinervata nervis primariis interioribus (1.0–)1.5–3.5(–4.5) cm supra basim divergentibus. Inflorescentia axillaris ca. 5–8 mm pedunculata, floribus 10–50(–80) subumbellatim aggregatis, pedicellis (6–) 10–25 mm longis. Hypanthium fructiferum (ad torum) 6–7 mm longum; calycis tubus ca. 2 mm longus. Petala asymmetrice obovata apice hebeti-obtusa. Stamina isomorphica glabra; antherarum thecae declinatae subulatae 7.5–8 mm longae, connectivi dente basali 1 mm longo robusto acuto, appendice dorsali 2–3 mm longa. Semina cuneata 0.5–1 mm longa.

Shrub or small tree 2–3.5 m tall. Cauline internodes and distal branchlets ± flattened or compressed and 2-edged, glabrous throughout. Older stems with prominent corky leaf scars, the bark cracking and becoming somewhat corky in age. Leaves of a pair somewhat unequal in size, the larger leaf at each node (11–) 14–26 cm long and 7–12.5 cm wide, the smaller leaf 9–19.2 cm long and 5.5–9.5 cm wide; blades chartaceous, glabrous, entire, broadly elliptic, elliptic-lanceolate or rarely varying to oblanceolate, acuminate to cuspidate apically and acute to rarely obtuse basally, 5-plinerved with a network of elevated secondary nerves, the innermost pair of primary nerves diverging from the median nerve (1.0–)1.5–3.5(–4.5) cm above the petiole/laminar junction, the outer pair of primaries diverging at or near the base of the blade; petioles (0.7–)1.5–4.0 cm long. Inflorescence a congested multiflowered, axillary umbel arising from short branchlets 5–8 mm long. Pedicels (6–)10–25 mm long, flexuous and glabrous. Hypanthia (at anthesis) campanulate, glabrous, 3–5 mm long to the torus. Calyx tube ca. 2 mm long, spreading and flangelike; calyx lobes depressed and evident as low, truncate undulations; calyx teeth obsolete. Petals glabrous, reportedly white to pink but drying yellow, obovate, ± obliquely rounded apically, entire, 10–13 mm long and 8–9 mm wide. Stamens isomorphic to anisomorphic; filaments declinate, ligulate, 7–10 mm long and 1 mm wide; anthers geniculate, 7.5–8 mm long, subulate and curved distally, the connective modified at the base on the dorsal side into an erect spur 1 mm long and a rigid acuminate appendage (2–3 mm long) directed ± parallel to the anther thecae. Style glabrous, ± declinate, 8–8.5 mm long; stigma punctiform. Hypanthia (at maturity) campanulate, ecostate and becoming papery or somewhat corky in age, 6–7 mm long to the torus and 6–8 mm wide. Seeds brown, minutely asperulate, cuneate and conspicuously angled but not winged, mostly 0.5–1 mm long.

TYPE: PANAMA. COCLÉ: El Cope, on slope and ridge west of sawmill, 5 April 1978, *Hammel 2380* (CAS, holotype; MO, isotype).

Habitat and Distribution: Growing in cloud forests and along stream margins at elevations from 500 to 900 meters in the vicinity of Alto Calvario and El Cope de Veraguas, Panama. Flowering and fruiting specimens have been collected in January, April, May, and July.

This evidently local species was collected in an area which is already yielding a flora of high specific endemicity. Distinguishing features of this taxon include the completely glabrous vegetative and floral organs, the compressed, 2-edged distal branchlets, and the multiflowered, umbelliform, axillary inflorescences. The

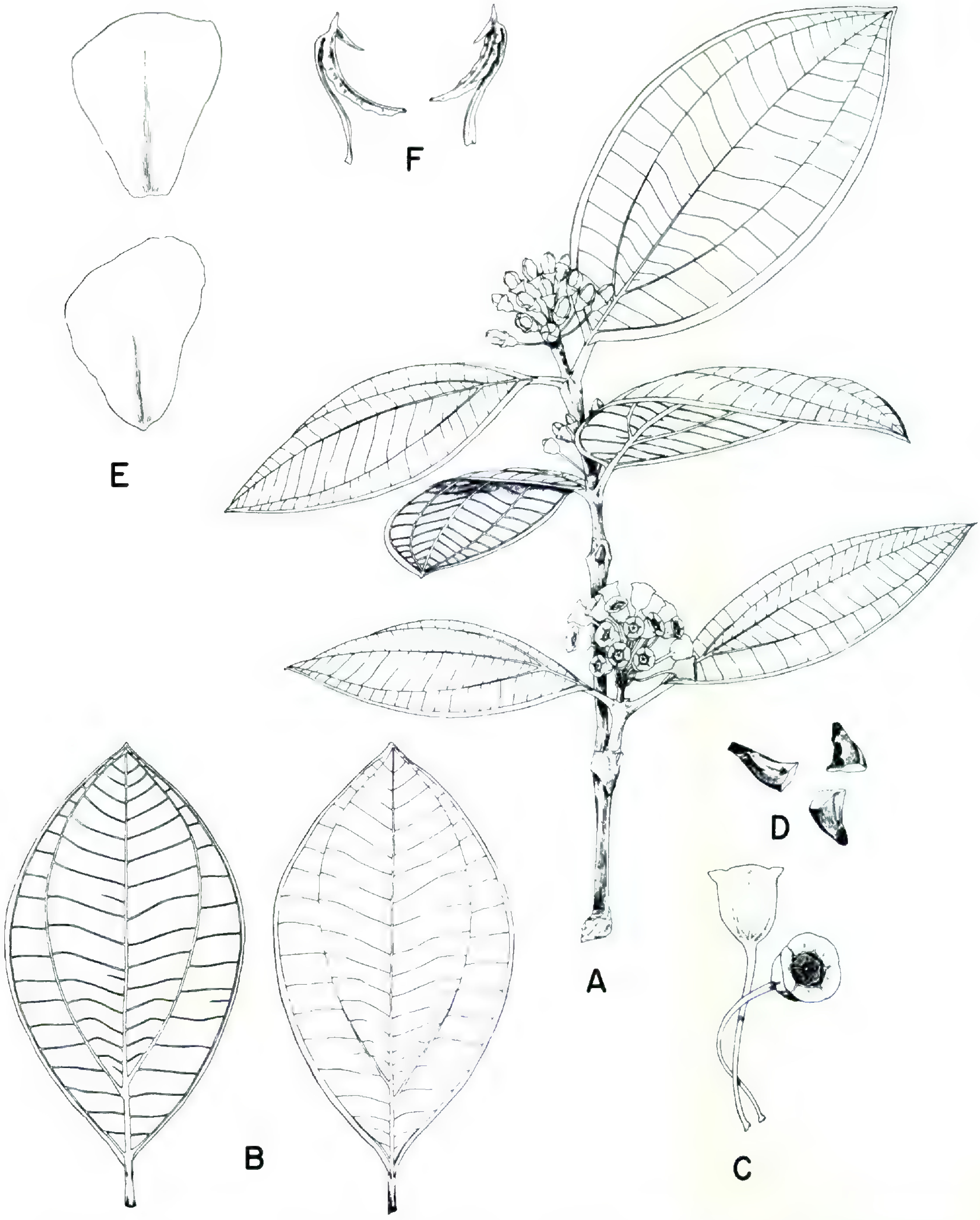

FIGURE 1. *Adelobotrys panamensis* Almeda.—A. Habit showing congested umbelliform inflorescences, ×¼.—B. Representative leaves, lower surface (left) and upper surface (right), ×¼.—C. Mature hypanthia, ×ca. 1.—D. Seeds, ×ca. 5.—E. Petals, ×1½.—F. Representative stamens (lateral view), ×ca. 1¼. (A–F from *Hammel 2380* and *Folsom 1234*.)

congested inflorescence which arises from a short stubby branchlet frequently appears terminal on new growth but its lateral position becomes obvious as vegetative growth continues after flowering of any one inflorescence.

Androecial morphology of this taxon is very much like that of *A. macrophylla*

Pilger, *A. marginata* Brade, and other South American species with a blunt or barely emarginate apex to the ascending connective appendage. Functional significance of the similar floral morphology among these species remains to be demonstrated. In the absence of clues from other structures it is tempting to utilize these floral characters in assessing relationships. On the other hand, the specified assemblage of South American species differs so markedly from *A. panamensis* in foliar size and shape, type of inflorescence, and vestiture that any statement regarding affinities would be tentative and ambiguous on the basis of present information.

Additional Specimens Examined: PANAMA. COCLÉ: 7 km N of El Cope de Veraguas, *Folsom 1234, 3219* (both CAS, MO). New works at Aseradera Rivera, Alto Calvario, *Folsom 2337* (CAS, MO). Area around Rivera Sawmill, Alto Calvario, *Folsom 4117* (CAS, MO). 8 km above El Cope, *Hammel 799* (CAS, MO). Top of El Petroso, *D'Arcy 11353* (CAS, MO). North of El Cope, *D'Arcy 11291* (CAS, MO).

2. **Adelobotrys adscendens** (Sw.) Triana, Trans. Linn. Soc. London 28: 67, *pl. 5, fig. 56.* 1871.

Melastoma adscendens Sw., Fl. Ind. Occ. 2: 772. 1798. TYPE: Jamaica, without exact locality, *Swartz s.n.* (holotype presumably at Stockholm (S) but not seen; C, probable isotype).
Davya guianensis DC., Prodr. 3: 105. 1828. TYPE: French Guiana, without exact locality, *Patris s.n.* (G-DC, holotype; P, isotype).
D. adscendens (Sw.) Griseb., Fl. Brit. W. Ind. 265. 1860.
Adelobotrys guianensis (DC.) Gleason, Brittonia 1: 141. 1932.

Scandent woody vine or hemiepiphyte adhering to tree trunks by adventitious roots. Internodes and distal branchlets terete, pubescent to glabrate but young shoots, petioles, immature hypanthia, pedicels, and branches of the inflorescence beset with a sparse to dense covering of brown malpighiaceous hairs. Leaves of a pair somewhat unequal in size but otherwise similar in shape and vestiture; blades chartaceous, entire to denticulate, (5.6–)7.5–22 cm long and 3–13.5 cm wide, ovate, elliptic-ovate, or subrotund, acute to short-acuminate apically and broadly rounded to cordate basally, 5–7-nerved, glabrous above at maturity, but with a sparse to moderate covering of malpighiaceous hairs mostly restricted to the elevated primary nerves below; petioles 1–3.5(–5.5) cm long and 1.5–2.5 cm wide. Inflorescence a terminal panicle mostly 14–40 cm long composed of umbelliform clusters of 2–6(–12) flowers; bracteoles sessile, entire, early deciduous, 1–3 mm long and 0.5–1.5 mm wide, linear-lanceolate to subulate. Pedicels 1–5 (–7) mm long. Hypanthia (at anthesis) subcylindric to suburceolate, 3–5 mm long to the torus. Calyx tube 1–2 mm long, ± spreading and flangelike; calyx lobes obsolete; calyx teeth usually obsolete or minute and inconspicuous when present. Petals glabrous, white to pale pink but yellow on drying, obovate and rounded to oblique apically, entire, 10–12 mm long and 7–8 mm wide. Stamens isomorphic or dimorphic; filaments declinate, ligulate, white when fresh but frequently drying blue or blue green, 7–10 mm long and 1 mm wide; anthers geniculate, 5–10 mm long, glabrous, yellow, linear-subulate and tipped with a dorsally inclined solitary pore, the connective ± thickened dorsally and modified into a short (0.5–1 mm) ascending acuminate spur and a bifid caudiform appendage (3.5–4 mm) directed ± parallel to the anther thecae. Style glabrous, ± declinate but incurved apically, 7–9.5 mm long; stigma punctiform. Hypanthia (at maturity) urceolate, promi-

nently 10-ribbed, 6–9 mm long and 6–8 mm wide. Seeds pale brown, obscurely foveolate, linear-cuneate, winged at the apex but tapered and ± caudate at the base, mostly 1.5–2.5 mm long.

Habitat and Distribution: Growing in wet forests from sea level to about 1,000 meters elevation. This, apparently, is the most widespread species of *Adelobotrys,* ranging from southern Mexico and Jamaica through northern South America to the Amazon basin. It flowers and fruits sporadically all year.

Populations of this species from Peru (Macbride, 1941), British Guiana (Wurdack, 1970), and Jamaica (Gleason, 1932) are reported to have dimorphic stamens. Specimens from British Honduras (*Gentle 8646*), Mexico (*Mexia 9151*), Costa Rica (*Schnell 582*), and Panama (*Mori & Kallunki 2354*) also exhibit differentiation in staminal size but the frequency of this dimorphism among Mexican and Central American populations is unclear and needs further study.

Through its broad range, this species is represented by a number of local but taxonomically insignificant variants differing in leaf size and shape, density of cauline and foliar pubescence, inflorescence size, and development of calyx teeth. The most notable variants among specimens studied are from the provinces of Colón, Panamá, and Veraguas in central Panama. These stand out by virtue of their copiously pubescent hypanthia, more congested umbelliform clusters of the inflorescence, and ± elevated, deltoid calyx teeth which conspicuously project beyond the calyx tube when in bud.

Representative Specimens: MEXICO. OAXACA: Sierra San Pedro Nolasco, Talea, *Jurgensen 865* (BM, G, K, US). Distrito Choapan, Yaveo, *Mexia 9151* (CAS, F, G, GH, MO, NY, U). GUATEMALA. ALTA VERAPAZ: 8–10 mi NW of Cubilguitz along Río Icvolay, *Steyermark 45042* (F). Sebol, ca. 1 km W of village, *Contreras 4509* (LL). Chahal, near airport, *Contreras 7994* (LL). IZABAL: Between Virginia and Lago Izabal, Montaña del Mico, *Steyermark 38869* (F). Near Entre Ríos, *Standley 72589* (F). Vicinity of Puerto Barrios, *Standley 25000* (GH, US). PETÉN: La Esperanza on Cadenas Rd., *Contreras 6506* (DS, F, LL). BELIZE. EL CAYO: High ridge at base of hill, Hummingbird Hwy., *Gentle 8646* (F, LL, MICH). STANN CREEK: Big Eddy Ridge, *Gentle 3499* (A, MICH, NY). TOLEDO: Between Rancho Chico and Cockscomb, *Gentle 4317* (LL). HONDURAS. ATLANTIDA: Vicinity of San Alejo, *Standley 7911* (F). Lancetilla Valley, near Tela, *Standley 54162* (F, US). COLÓN: Guarunta, Wispernini Camp, *von Hagen & von Hagen 1379* (F, NY). CORTÉS: Ca. 6 km N of Rancho Agua Azul, *Williams & Molina 17777* (F, GH). NICARAGUA. COMARCA DEL CABO: Between Waspán and Puerto Cabezas, *Nelson 4826* (MO). CHONTALES: Vicinity of Santo Domingo, *Bunting & Licht 1186* (F). RÍO SAN JUAN: Near Caño Chontaleño, *Neill 3358* (CAS, MO). RIVAS: Volcán Madera, *McGillivary 103* (F). ZELAYA: Vicinity of El Recreo, on Río Mico, *Standley 19747* (F). 3.1 km N of base camp 3.6 km SE of Cerro San Isidro, *Proctor et al. 27177* (NY). COSTA RICA. ALAJUELA: 3 km NNE of Bijagua, *Burger & Baker 9834* (F). CARTAGO: Valle Escondido, *Schnell 656* (F, US). HEREDIA: E of Puerto Viejo, *Godfrey* (FSU). Tirimbina, *Proctor 32250* (LL). LIMÓN: Vicinity of Guápiles, *Standley 37299* (US). Barra de Colorado, *Schnell 582* (F, US). PUNTARENAS: Helechalis, *Schnell 488* (US). Esquinas Forest Preserve, *Allen 5759* (DS, F, FSU, GH). Rd. to tower above Golfito, *Almeda et al. 3090* (CAS). 6–9 km E of Salitre, *Almeda & Nakai 4083* (CAS). Hills N of Palmar Norte, *Croat 35179* (MO). SAN JOSÉ: 1–3 km SW of Quizarrá, *Almeda & Nakai 4140* (CAS). Vicinity of El General, *Skutch 3190* (GH, MO, NY). PANAMA. BOCAS DEL TORO: Almirante region, Cricamola Valley, *Cooper 201* (F, NY). CANAL ZONE: Barro Colorado Island, *Foster 2090* (MO). COCLÉ: 2 km W of Cerro Pilón, *Sullivan 452* (CAS, MO). 3 km NE of El Valle, *Mori & Kallunki 2964* (MO). COLÓN: Summit of Cerro Santa Rita, *Allen 5106* (BM, BR, G, MO, NY). DARIÉN: Between Río Perecenico and Rancho Frio, *Duke & Elias 13887* (MO). Cerro de Garagara, Sambu basin, *Pittier 5667* (US). PANAMÁ: El Llano-Cartí Rd., 17.5 km from Panamerican Hwy., *Mori et al. 4606* (MO). Slopes of Cerro Campana, *Wilbur & Weaver 11303* (MICH, MO). Rd. to Altos de Pacora, *Mori & Kallunki 2354* (MO). Cerro Jefe, *Duke 8001* (MO). VERAGUAS: Río Segundo Brazo, *Maas & Dressler 1671* (U, US).

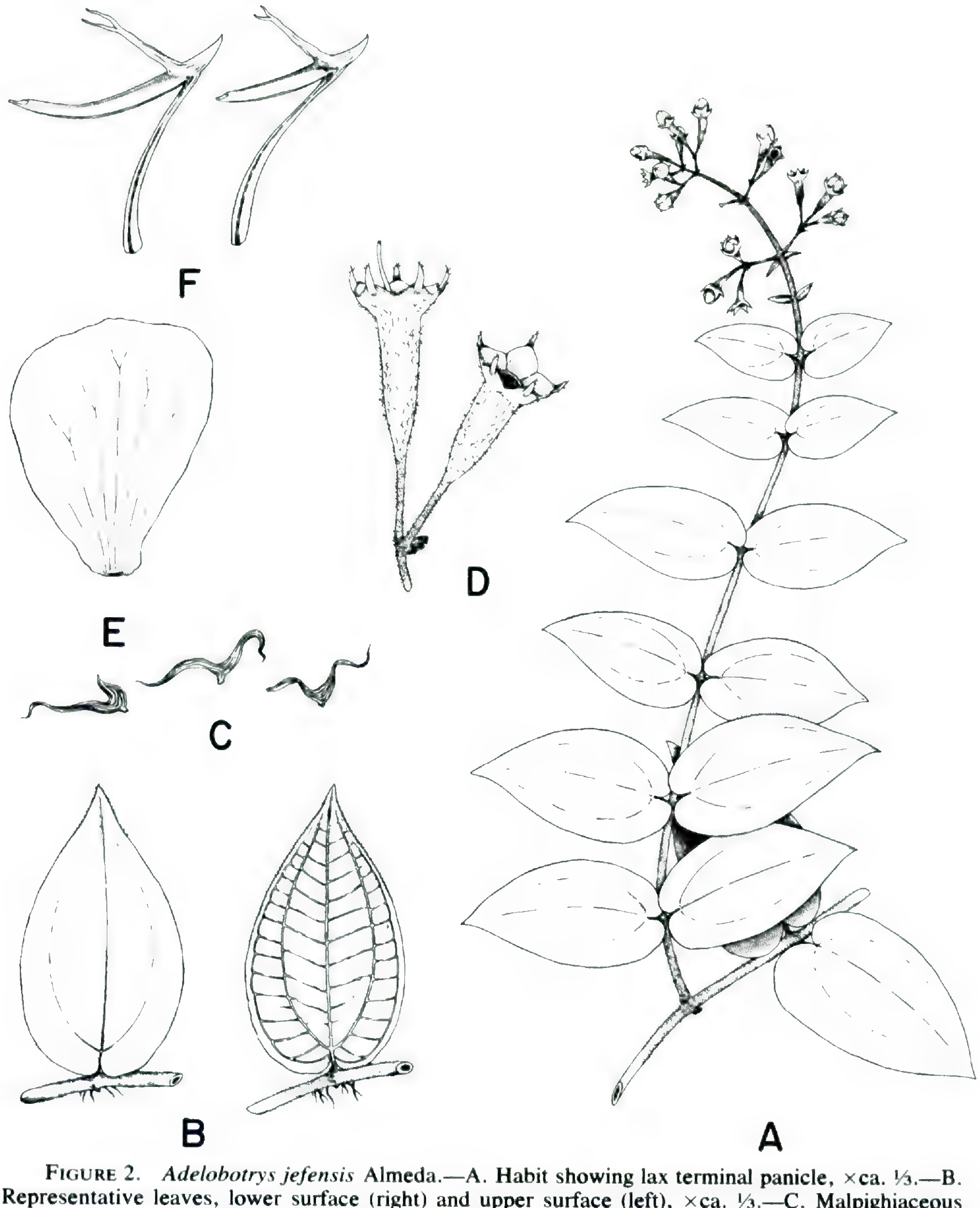

FIGURE 2. *Adelobotrys jefensis* Almeda.—A. Habit showing lax terminal panicle, ×ca. ⅓.—B. Representative leaves, lower surface (right) and upper surface (left), ×ca. ⅓.—C. Malpighiaceous trichomes, ×4.—D. Immature hypanthia, ×2.—E. Petal, ×2½.—F. Representative stamens (lateral view) showing larger stamen (left) and smaller stamen (right), ×ca. 2½. (A–F from the holotype.)

3. **Adelobotrys jefensis** Almeda, sp. nov.—FIG. 2.

Caulis scandens primum sicut foliorum subtus venae primariae inflorescentia hypanthiaque dense vel modice setulosi pilis castaneis malpighiaceis. Petioli (1–)2–3 mm longi; lamina 2.8–4.6 × 1.3–2.8 cm, elliptica vel ovato-elliptica apice acuto vel breviter acuminato basi cordata vel auriculata, chartacea et integra vel obscure denticulata. Panicula laxe multiflora, pedunculo usque ad 4.5–8 cm longo,

pedicellis ad anthesim 3–5 mm longis. Hypanthium (ad torum) 5 mm longum; calycis tubus 0.5–1.0 mm longus, lobis interioribus 1.5 mm longis late ovatis, dentibus exterioribus prominentibus robustis 1.5–2.0 mm eminentibus. Petala eciliata glabra, 7–9 × 5–6 mm obovata apice ± rotundata. Stamina anisomorphica glabra; antherarum thecae 3.5–4.0 vel 4.5–5.0 mm longae, dente basali 1–1.5 mm longo robusto acuto, appendice adscendenti 2.5–3 mm libera apice caudato-bifido. Fructus maturus ignotus.

Scandent vine adhering to bark of the host tree by adventitious roots. Internodes and distal branchlets terete, moderately pubescent to glabrate, young shoots, petioles, immature hypanthia, bracteoles, pedicels, and branches of the inflorescence copiously beset with ferrugineous malpighiaceous hairs. Leaves of a pair equal to slightly unequal; blades chartaceous, entire to bluntly denticulate, 2.5–4.6 cm long and 1.3–2.8 cm wide, elliptic to elliptic-ovate, acute to short-acuminate apically and cordate-clasping to auriculate basally, 3-plinerved with an additional submarginal pair, the secondary nerves usually evident below as prominulous ridges, glabrous above at maturity or with trichomes restricted to the median nerve, with a sparse to moderate covering of malpighiaceous hairs largely restricted to the primary and secondary nerves below; petioles (1–)2–3 mm long and 1 mm wide. Inflorescence a terminal ± diffuse panicle mostly 4.5–8 cm long, the ultimate units consisting of solitary flowers or umbelliform clusters of 3–4 flowers; bracteoles sessile, membranous, entire, markedly reduced in size upward, 1.5–4 mm long and 0.5–1.5 mm wide, linear-lanceolate to subulate. Pedicels 3–5 mm long. Hypanthia (at anthesis) cylindric to narrowly campanulate, 5 mm long to the torus. Calyx tube 0.5–1.0 mm long; calyx lobes spreading, broadly ovate or hemispheric, acute to rounded apically, entire or occasionally ciliate, 1.5 mm long and 1.5–2.0 mm wide; calyx teeth lanceolate, 1.5–2.0 mm long and conspicuously projecting beyond the calyx lobes. Petals glabrous, reportedly orange red, obovate and rounded apically, entire, 7–9 mm long and 5–6 mm wide. Stamens anisomorphic; filaments alternately 5.5 mm and 6–6.5 mm long; anthers alternately 3.5–4.0 mm and 4.5–5.0 mm long, the connective modified dorsally into an erect spur 1–1.5 mm long at the junction of the anther and filament and a bifid appendage (2.5–3 mm long) directed upward and ± perpendicular to the anther thecae. Style glabrous, erect or slightly declinate, 4–5 mm long; stigma ± truncate. Mature hypanthia and seeds not seen.

TYPE: PANAMA. PANAMÁ: La Eneida, low forest at 800 m, 2 September 1974, *Maas, Dressler & Kennedy 1564* (U, holotype; CAS, photograph; US, isotype).

This species is distinguished by the combination of small (2.5–4.6 × 1.3–2.8 cm), cordate-clasping leaves, short petioles, diffuse paniculate inflorescences, highly reduced bracteoles, elongate hypanthia, prominent calyx teeth, and anisomorphic stamens. While known only from the type collection, *A. jefensis* is confidently described as a new species. It is perhaps most closely related to the habitally similar *A. spruceana* Cogn. which it superficially resembles in foliar texture and hypanthial form. As presently understood, the latter species differs most conspicuously in the short (2–3 cm) congested bracteate inflorescence, stout simple trichomes along the foliar margins, and in the anther connective which is modified basally into a ± erect bifid spur and dorsally into a simple, distally emarginate appendage.

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NEW TAXA FROM THE UPLANDS OF WESTERN PANAMA[1]

Barry E. Hammel[2] and W. G. D'Arcy[3]

Abstract

Preliminary results of a recent expedition to Volcán Barú in Chiriquí Province have yielded two new species which are described here: *Verbesina baruensis* Hammel & D'Arcy (Compositae) and *Sicyos chiriquensis* Hammel & D'Arcy (Cucurbitaceae).

On a recent expedition[4] to Volcán Barú in Chiriquí Province, Panama, we encountered numerous first records of vascular plants for Panama and several new species, two of which are described here. A full list of vascular plants known from the volcano above ca. 2,000 m is now being prepared and will be published later.

Verbesina baruensis Hammel & D'Arcy, sp. nov.—Fig. 1.

Arbor ad 25 m alta, ad 40 cm diametro ad altitudinem pecti; ramunculis lanatis. Folia alternantes, late lanceolata ad 60 cm longa, 30 cm lata, basim truncata vel leviter cordata, saepe obliqua; petiolis 10–12 cm longis, confertim lanatis. Inflorescentia late paniculata, capitulis globosis, basim truncatis, involucro 1.5–2 cm lato; paleis 10–12 mm longis, capitulis ca. 25 radios includentibus, tubo corollae ad 2 mm longo, pubescenti, ligula aurea vivida, lanceolata, ad 4 mm lata; corolla florum disci 6–7 cm longa, glandulosa pubescente basim ⅓. Achinium ad 7 mm longum, alis ca. dimidio latitudino corpi, aristis validis, triangularibus, ca. ⅔ longitudino corpi.

Tree to 25 m tall, 40 cm d.b.h.; trunk gray, smooth; wood white; young stems woolly with yellow brown hairs. *Leaves* alternate, broadly lanceolate; blade to 60 cm long, 30 cm wide, the base shallowly cordate or truncate, but acuminate near the inflorescence, often oblique, the margin with ca. 5 short teeth per cm, tomentose below, woolly on the veins, scabrous above; petioles 10–12 cm long, densely woolly. *Inflorescence* a broad panicle 15–20 cm across; pedicels 1–10 cm long, woolly. *Heads* globose, truncate at the base, the involucre 1.5–2 cm wide; involucral bracts approximating 2 whorls, the outer bracts wider and shorter than the inner more lanceolate bracts; paleas 10–12 mm long, folded around the floret; ray florets fertile, bright orange yellow, ca. 25 per head, the corolla to 20 mm long, abruptly expanded from the short, pubescent tube (2–4 mm long) into a lanceolate ligule to 4 mm wide; disc florets fertile, yellow green, the corolla 6–7 mm long, glandular pubescent on the lower ⅓, cylindrical, slightly and gradually expanded towards the top, the lobes shallow, less than 1 mm long; anthers black, ca. 3 mm long; style branches spatulate, pubescent at the tips. *Achene* body black, to 7 mm long, the wings ca. ½ the width of the body, one of them ciliate, the 2 stout triangulate awns ca. ⅔ the length of the body.

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[4] The field work was undertaken by the authors with the assistance of John E. Averett, University of Missouri, St. Louis, and four Earthwatch volunteers: Elaine C. Hill, Susan Schwartz, Helen M. and Oliver Wolcott. Housing and other help was provided by Maximo Menéndez Caballero and by the Panama Audubon Society.

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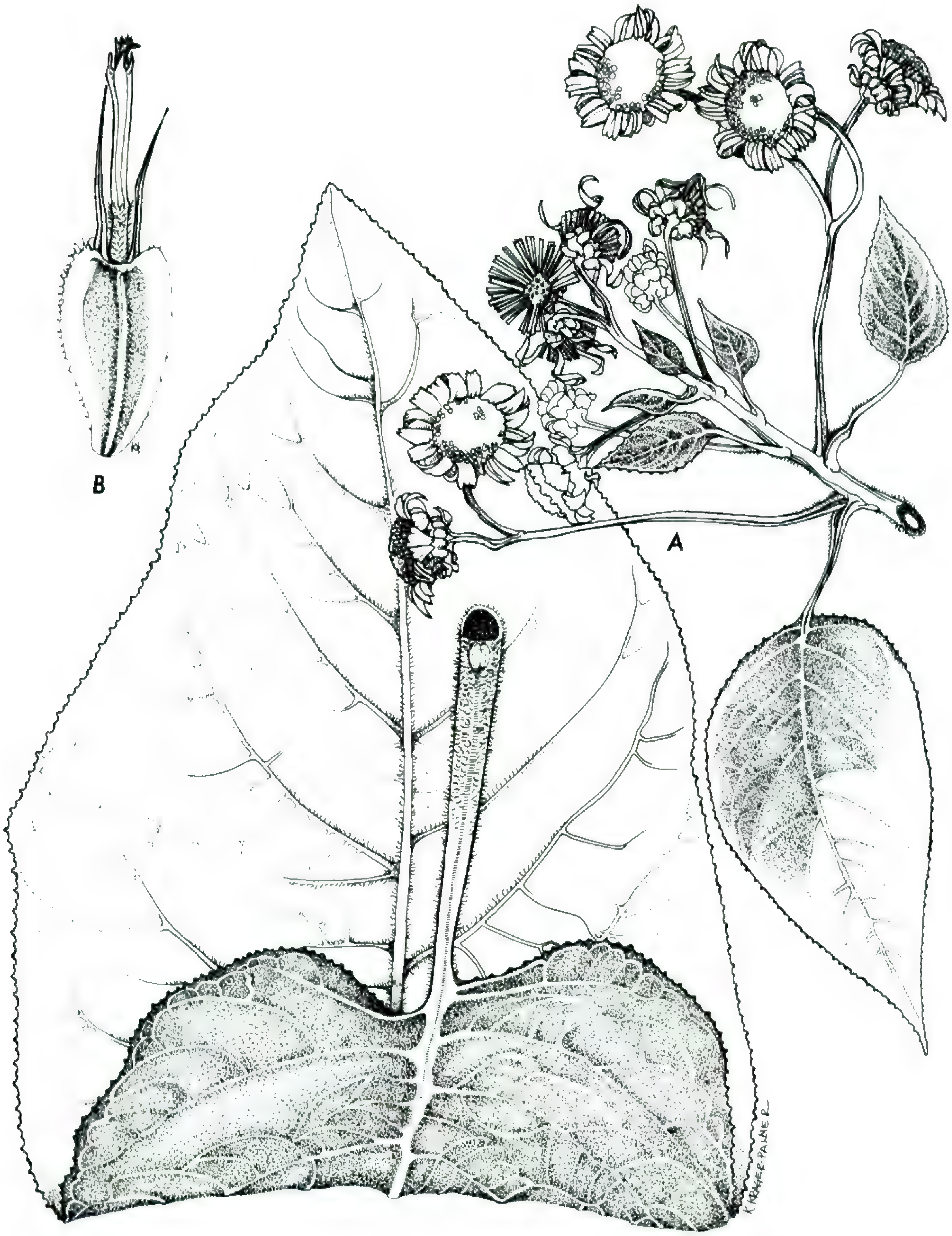

FIGURE 1. *Verbesina baruensis* Hammel & D'Arcy.—A. Habit (×½).—B. Disc floret (×4). [After *Hammel et al. 6449* (MO).]

TYPE: PANAMA. CHIRIQUÍ: Volcán Barú, E slope along road to summit near Potrero Muleto, 10400 ft, *Hammel et al. 6449* (MO, holotype; F, K, PMA, TEX, isotypes).

Other Specimens Seen: PANAMA. CHIRIQUÍ: E slope of Volcán Barú in wet forest N of Potrero Muleto along road to summit, 10200 ft, *Hammel 5643* (MO). E slope of Volcán Barú in wet forest N of Potrero Muleto along road to summit, 10400 ft, *Hammel 7490* (MO).

In the *Flora of Panama* treatment of the Compositae (D'Arcy, 1975) individuals of this species will key out to *Verbesina fuscasiccans* D'Arcy which is known only from central Panama. This species differs from *V. fuscasiccans* most obviously in overall size of the plants and in leaf shape. We saw no flowering material of *V. baruensis* under 15 m tall. The large cordate- to truncate-based leaf blades with densely woolly petioles are quite distinct from those of *V. fuscasiccans* which are long acuminate into a winged, slightly pubescent petiole. The flower heads of *V. baruensis* are about twice as large as those of the material of *V. fuscasiccans* studied, including its type.

Verbesina baruensis is common along several draws and slopes at about 3,000 m in high rainfall areas on the east and north side of the volcano. From a distance we saw the plants widely scattered along a few deep draws but we also found a number of almost pure stands of this magnificent composite tree. Flowering collections have been made between November and May and it seems likely that this tree blooms in all months of the year. Only the tallest plants were found in flower.

Sicyos chiriquensis Hammel & D'Arcy, sp. nov.—FIG. 2.

Labruscae monoeciae, foliis simplicibus 3–5 lobatis basim profunde cordatis. Inflorescentia staminata axillaris, racemosa, de inflorescentiis foemineis separata; inflorescentia pistillata axillaris capitata. Flos staminatus 5-merus campanulatus 4–6 mm longus, 3–4 mm latus, lobis calycis linearibus 1 mm longis, staminibus 5, filamentis connatis sed apice leviter divergentibus, antheris reniformibus, prope medio insertis. Flos pistillatus 5 merus salverformis, perianthio perianthiis staminatis minori, ca. 3 mm longo, stigma 2 vel 3 lobata. Fructus in fasciculis ad 4 cm diametro retentes, maturi samaroidei elliptici ca. 2 cm longi, 1.5 cm lati papyracei praeter partem seminis, cristis binis centralis longitudinalis semine obtectis margineque irregulariter serratim, dentibus late triangularis 2–4 mm longis, aristis recurvatis tectis.

Slender monoecious *vines*; stems glabrous to slightly pubescent when young. *Leaves* simple, pentagonal in outline, 5–15 cm long, equally wide, primarily 3-lobed to ⅔ the distance to the midrib, the lower 2 lobes with 1 or 2 secondary enations, the leaf base deeply cordate and hastate, the margin undulate dentate with ca. 3 teeth per cm, the blade scabrous above with scattered short hairs, more numerous toward the margin, hirsute below, prominently so on the veins; petioles 1–22 cm long, pubescent along one side; tendrils 1–2 branched. *Staminate inflorescence* axillary, racemose, 2–6 cm long, few(ca. 10)-flowered, floriferous in the upper ⅓, the pedicels to 2 cm long. *Flowers* yellow green, campanulate, 4–6 mm long, 3–4 mm wide; lobes of the calyx 5, linear, 1 mm long; corolla 5-merous, merging imperceptibly with the calyx tube, divided to ⅔ the length, the lobes broadly lanceolate, nearly erect, incurved, densely papillose-pubescent inside, 3–7-nerved; stamens 5, the filaments united into a column equalling or slightly exceeding the floral tube, free and divergent for ca. 1 mm at the summit, the anthers reniform, attached near the middle. *Pistillate inflorescence* axillary, capitate, 15–20 flowers sessile on the end of a peduncle ca. 2 cm long; perianth smaller than that of the staminate flowers, ca. 3 mm long, 5-merous, salverform;

FIGURE 2. *Sicyos chiriquensis* Hammel & D'Arcy.—A. Habit (×½).—B. Fruit (×2). [After *Hammel et al. 6823* (MO).]

calyx lobes linear, 1 mm long; corolla lobes lanceolate-triangular, 2 mm long, papillose inside; stigma 2- or 3-lobed, the flat elliptic ovary with a low, longitudinal ridge on the center of each face, these ridges and the margin of the ovary toothed, the teeth capped with 4 recurved barbs. *Fruits* samaralike, tan to lustrous brown,

ca. 2 cm long, 1.5 cm wide, paper thin except in the area of the seed, the central longitudinal ridges over the seed and margin of the samara irregularly serrate, the teeth broadly triangular, 2–4 mm long, capped with recurved barbs, the fruits held by these barbs in pendulous clusters to 4 cm in diameter; seed adherent to the fruit wall.

TYPE: PANAMA. CHIRIQUÍ: Along small stream in backyard of Audubon cabin, Bambito, 6200 ft, *Hammel et al. 6823* (MO, holotype; DUKE, F, K, MICH, PMA, US, isotypes).

Sicyos chiriquensis is quite distinct from other Panamanian Cucurbitaceae in its paper-thin samaroid fruits. Although these represent an extreme otherwise unknown in the genus, somewhat flattened fruits and armed fruits with recurved barbs on the spines do occur. This complex of characters suggests that animal and perhaps torrent dispersal have been important in the evolution of *Sicyos*.

To the casual observer *Sicyos chiriquensis* might easily appear sterile while in full flower and fruit. The small green flowers and leaflike clusters of fruits are very inconspicuous. The type locality has been visited by many biologists in recent years but this appears to be the plant's first gathering. The collection was made in April on the wet northwest side of Volcán Barú near Cerro Punta.

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NEW SPECIES OF *CONNARUS* (CONNARACEAE) FROM PERU[1]

ENRIQUE FORERO[2]

ABSTRACT

Two new species of Connaraceae from Peru—*Connarus bracteoso-villosus* Forero and *Connarus elsae* Forero—are described and illustrated.

In the course of studying the Neotropical species of Connaraceae I have found several novelties. This paper includes two interesting species of *Connarus* from Amazonian Peru.

Connarus bracteoso-villosus Forero, sp. nov.—FIG. 1.

Species insignis axibus inflorescentiae dense villosis et bracteis elongatis (usque 0.5 cm longis) dense villosis ab congeneribus distincta.

Shrub 1 m tall, branchlets grey; conspicuously lenticellate, the lenticels small. Leaves imparipinnate, 7–9 foliolate; pulvinulus 5–7 mm long; petiole cylindric, glabrous, (7–)8 cm long; rachis cylindric, glabrous, (7.5–)11.5 cm long; leaflets 5–11.5 cm long, 2.5–4.5 cm wide, elliptic, chartaceous, glabrous, rounded to angustate at the base, acuminate at the apex; petiolule 4–5 mm long; midrib somewhat impressed above, prominent below, the lateral veins 9–10 pairs, diverging from the midrib at angles of 70°, anastomosing diffusely near the margin, slightly prominent below. Inflorescence paniculate, congested; rachilla up to 20 cm long, characteristically densely villous; bracts characteristically long, up to 5 mm, densely villous. Flowers pedicellate; pedicel 5 mm long, villous, thick; sepals 3–3.3 mm long, 1.8–2 mm wide, ovate-elliptic, conspicuously punctate, villous without, villous towards the apex within, the apex acute, densely villous; petals 4–4.2 mm long, 1.3 mm wide, subspatulate, densely glandulose without, glandulose in the upper half within, the margin glandulose, and with 1–3 dots in some (usually 2) of the petals, the rest epunctate; stamens 10, 5 short, 2.2 mm long, 5 long, 3 mm long, glandulose, the tube ca. 0.5 mm long, the anthers globose, ca. 0.4 mm diameter; ovary densely villous. Fruit unknown.

TYPE: PERU. DEPTO. HUÁNUCO: Provincia Pachitea, Distrito Honoria, Bosque Nacional de Iparia, región de "bosque seco tropical" a lo largo del Río Pachitea cerca del campamento Miel de Abeja (1 km arriba del pueblo de Tournavista o unos 20 km arriba de la confluencia con el Río Ucayalí), en bosque bajo en la carretera Miel de Abejas, arbusto 1 m, flores amarillas pálidas, 5 Jun. 1967, *Schunke 2040* (F, holotype).

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[1] Acknowledgments are due to the John Simon Guggenheim Memorial Foundation for financial support. Margaret Kurzius prepared the excellent illustration of *Connarus bracteoso-villosus*.

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ANN. MISSOURI BOT. GARD. 68: 218–221. 1981.

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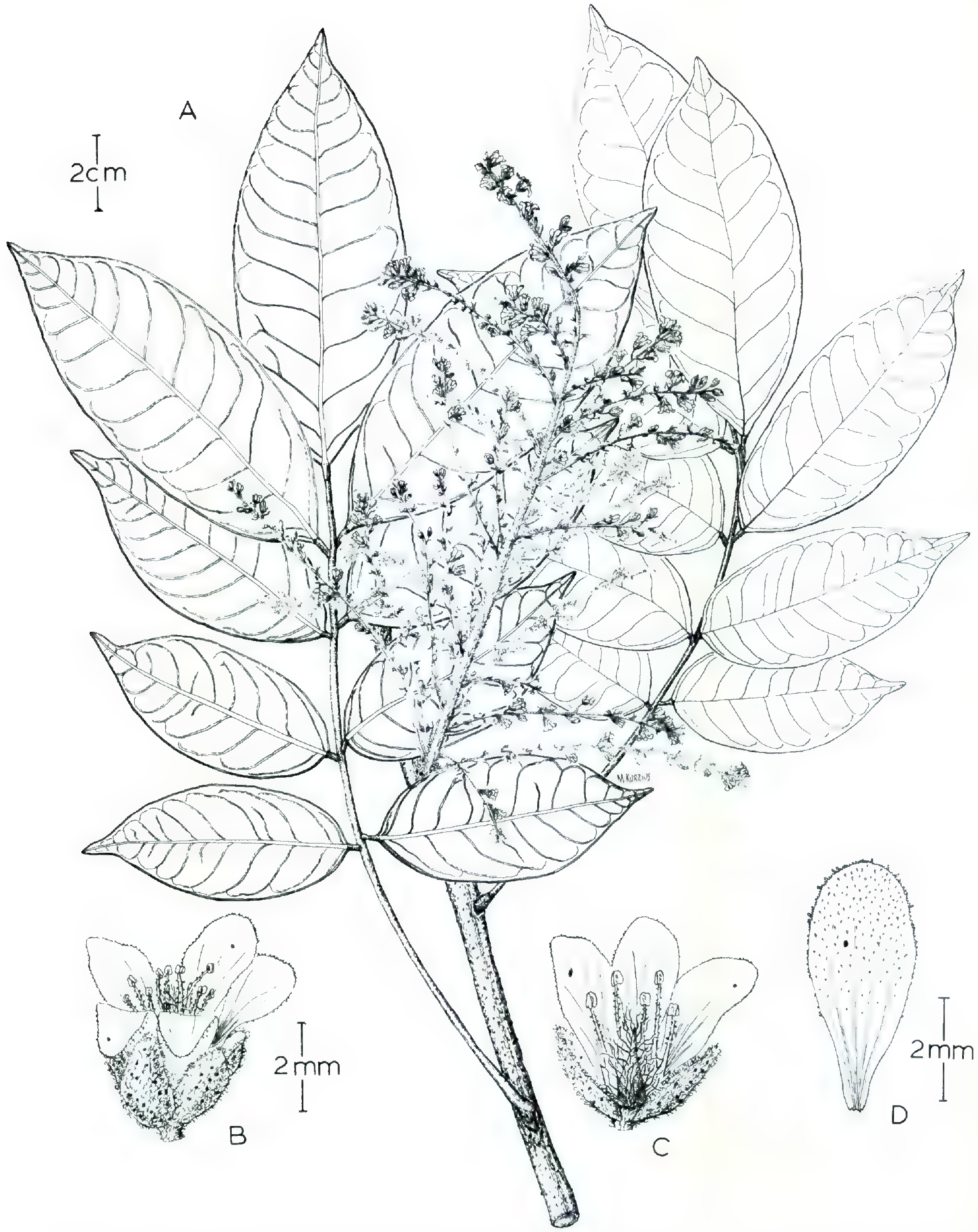

FIGURE 1. *Conarus bracteoso-villosus* Forero, *Schunke 2040* (F).—A. Habit (×½).—B. Flower (×6).—C. Flower section (×6).—D. Petal (×7).

This species is known so far only from the type locality in the Department of Huánuco, Peru, occurring in low forest at altitudes between 300 and 400 m.

The affinities of this very distinct species are uncertain. It can be easily distinguished from any other species of the genus by the very long bracts which are densely villous and by the densely villous pubescence of the inflorescence.

FIGURE 2. Holotype of *Connarus elsae* Forero, *Plowman 6017* (F). (Photo: Dr. María Lebrón Luteyn, New York Botanical Garden.)

Connarus elsae Forero, sp. nov.—FIG. 2.

Ab speciebus affinis *C. punctatus* Planch. petalis epunctatis foliolorum basium angustata vel rotundata, stipite fructis brevioribus differt.

Small tree or shrub, up to 8 m tall; branchlets puberulous, conspicuously lenticellate, the lenticels small. Leaves imparipinnate, (3–)5(–7)-foliolate; pulvinulus 3–5 mm long; petiole glabrous, (2–)3–7.5 cm long; rachis glabrous, (1–)2.5–11.5 cm long; leaflets (5–)7–12(–15) cm long, (2.4–)2.7–5 cm wide, elliptic or narrowly elliptic, chartaceous, glabrous, attenuate or somewhat rounded at the base, acuminate at the apex; petiolule 2–5 mm long; midrib impressed above, prominent below, the lateral veins 8–10 pairs, diverging from the midrib at angles of 45°–60°, anastomosing irregularly near the margin, slightly prominulous below. Inflorescence paniculate; panicules fasciculate in groups of 1–3 per axil; rachilla (2–)4–9(–15) cm long, tomentose; bracts conspicuous, black dotted. Flowers pedicellate; pedicel 3–4 mm long, puberulous; sepals 2.5–3 mm long, 1–1.5 mm wide, ovate, sparsely punctate, puberulous without, glabrate within, the apex obtuse; petals 3.5–5 mm long, 1.3–1.5 mm wide, obovate-lanceolate, epunctate, sparsely puberulous and glandulose without, sparsely glandulose within; stamens 10, 5 short, 1.5–2 mm long, 5 long, 2–3.2 mm long, with few glandular hairs towards the apex, the anthers globose, 3–4 mm in diameter. Follicle stipitate; stipe 2–5 mm long; fruit 2–2.5 cm long, 1.4–1.7 cm wide, glabrous or glabrate, outside, densely puberulous inside; calyx in fruit persistent.

TYPE: PERU. DEPT. SAN MARTÍN: Provincia San Martín, road from Puente Colombia to Shapaja, along Río Mayo, shrub 3 m tall on steep bank in full sun, fruits green, 30 Apr. 1976, *Plowman 6017* (F, holotype).

Additional Collections Examined: PERU. SAN MARTÍN: Juan Jui, alto río Huallaga, Oct. 1934, *Klug 3855* (BM, F, GH, K, MO, NY, US). Tarapoto, Apr. 1856, *Spruce s.n.* (K). Alto Río Huallaga, Dec. 1929, *Williams 5670* (F, US), *5733* (F, G). Río Mayo, Tarapoto, 14 Dec. 1929, *Williams 6209* (BM, F), *6214* (F). Rumizapa, near Tarapoto, Dec. 1929, *Williams 6808* (F, US).

This species is known from the Department of San Martín, Peru, where it occurs above 280 m elevation. It has often been confused with *Connarus punctatus* from which it differs by the epunctate petals, the shorter stipe, and also by the less numerous and somewhat smaller leaflets.

NOTES

CHROMOSOME NUMBERS OF MISCELLANEOUS ANGIOSPERMS

Chromosome numbers are reported in Table 1 for 20 collections representing 19 species. First reports are indicated by an asterisk preceding the name. Counts agreeing with those previously reported by other authors are not discussed any further.

Aponogetonaceae

Raven (1975) has suggested a base number of $x = 8$ for the family. *Aponogeton crispus* is the third chromosomally known species based on this number, whereas the high polyploid *A. natans* has been reported to have the apparently aneuploid numbers $2n = 76, 78, 92$ (Misra, 1972; Sharma & Chatterjee, 1967).

Eriocaulaceae

This family remains very poorly known cytologically with only the genus *Eriocaulon* previously known. Raven (1975) suggested a base number $x = 8$ for *Eriocaulon*, although numbers based on $x = 9$ and 10 have also been reported for four species (Cave, 1967; Erlandsson, 1942; Hedberg & Hedberg, 1977; Mehra & Sachdeva, 1971). The two current counts for *Syngonanthus* provide further support for a base number $x = 8$ for the family but also suggest that the family is cytologically diverse and well worth intensive cytological investigation.

Gesneriaceae

All the numbers here reported for species of this family agree with numbers previously reported for the respective genera. However, the report of tetraploidy for *Achimenes erecta* is of interest since polyploidy is rare in the family (Wiehler, 1971) although not previously unknown in the genus.

Gramineae

Ergrostis hypnoides, previously known from a single diploid count in the tropical portion of its range (Davidse & Pohl, 1972) is now shown to be tetraploid in the temperate portion of its range. This suggests a tropical origin for this species but more extensive sampling is obviously necessary.

Solanaceae

The chromosome number for the Panamanian endemic *Brunfelsia dwyeri* agrees with that previously reported for five other species and provides further evidence for a base number of $x = 11$ for the genus (Plowman, 1973).

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TABLE 1. Chromosome numbers and voucher information for miscellaneous angiosperms.

APONOGETONACEAE

* *Aponogeton crispus* Thunb. $n = 24$. SRI LANKA: Central Province, Nuwara Eliya District, Horton Plains, *Davidse 7616* (MO).

BUTOMACEAE

Limnocharis flava (L.) Buchn. $n = 10$. VENEZUELA: Guárico, ca. 50 km N of San Fernando de Apure, *Davidse, Agostini & Agostini 3820* (MO).

ERIOCAULACEAE

**Syngonanthus caulescens* (Poir.) Ruhl. $n = 13$. VENEZUELA: Guárico, ca. 32 km SSE of Calabozo, *Davidse 3771* (MO).

**Syngonanthus xeranthemoides* (Bong.) Ruhl. $n = 16$. VENEZUELA: Apure, between the Río Cinaruco and the Galeras de Cinaruco, *Davidse & González 12279A* (MO).

GESNERIACEAE

**Achimenes erecta* (Lam.) H. P. Fuchs. $n = 22$. JAMAICA: Portland Parish, Muriel's Rock, between Section and Hardware Gap, *Davidse & Proctor 3244* (MO).

Achimenes longiflora DC. $n = 11$. NICARAGUA: Managua, 27 km S of Managua along Hwy. 8, *Davidse & Pohl 2382* (MO).

Alloplectus tetragonus (Oerst.) Hanst. $n = 9$. COSTA RICA: Cartago, 2 km E of Muñeco, *Davidse & Pohl 1679* (MO).

Columnea linearis Oerst. $2n = 18$. NICARAGUA: Chontales, 8 km E of Villa Somoza along Hwy. 7, *Davidse 2734* (MO).

**Corytoplectus congestus* (Lind.) Wiehler. $n = 9$. VENEZUELA: Mérida, 66 km NE of Mérida along the Mérida-Azulita Rd., *Davidse 3239* (MO).

Gesneria aucaulis L. $n = 14$. JAMAICA: St. Catherine Parish, 2.1 mi SE of Bog Walk, *Davidse 3270* (MO).

Kohleria hirsuta (H.B.K.) Regel. $n = 13$. VENEZUELA: Distrito Federal, 7.0 km SW of Carayaca, *Davidse 2893* (MO).

Kohleria tubiflora (Cav.) Hanst. $n = 13$. NICARAGUA: Rivas, La Cuesta, 3 km NE of San Juan del Sur, *Davidse & Pohl 2284* (ISC, MO).

Kohleria tubiflora (Cav.) Hanst. $n = 13$. VENEZUELA: Barinas, 25 km NW of the Mérida intersection (just outside of Barinas) along road to Mérida, *Davidse 3187* (MO).

**Rhytidophyllum tomentosum* (L.) Mart. ex G. Don. $n = 14$. JAMAICA: St. Thomas Parish, just NW of Cedar Valley along road to Arntully, *Davidse 3262* (MO).

Sinningia incarnata (Aubl.) D. Denh. $n = 13$. EL SALVADOR: Libertad, 3 km E of La Libertad along Hwy. 2, *Davidse & Pohl 2056* (MO).

GRAMINEAE

**Eragrostis hypnoides* (Lam.) B.S.P. $n = 20$. UNITED STATES: Missouri, St. Charles Co., ca. 1 mi SW of the bridge at the intersection of U.S. Hwy. 40 and the Missouri River, *Davidse 3553* (ISC, MO).

Eragrostis pectinacea (Michx.) Beauv. $n = 30$. UNITED STATES: Missouri, St. Charles Co., ca. 1 mi SW of the bridge at the intersection of U.S. Hwy. 40 and the Missouri River, *Davidse 3554* (ISC, MO).

Sporobolus asper (Michx.) Kunth. $n = 27$. UNITED STATES: St. Louis, *Davidse 3671* (MO).

LAURACEAE

Cassytha filliformis L. $n = 24$. BELIZE: Belize District, ¾ mi in from Western Hwy. on Fergerson Bank, *Dwyer 12803* (MO).

SOLANACEAE

**Brunfelsia dwyeri* D'Arcy. $2n = 22$. PANAMA: Panamá, Cerro Jefe, *Gentry 4883* (MO).

* First report or different count.

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—*Gerrit Davidse, Missouri Botanical Garden, Post Office Box 299, St. Louis, Missouri 63166.*

A NEW SPECIES OF *HERNANDIA* (HERNANDIACEAE) FROM PANAMA

Hernandia hammelii D'Arcy, spec. nov.

Arbor 15–20 m alta, ligno leni, virguli crassis, cicatrices petiolorum circulares conspicuas ferenti, ramunculis parum gracilioribus nigris siccantibus; folia ovata vel elliptica, 6–8 cm longa, 2.5–4 cm lata, apice breve accuminata, basim rotundata, glabra, coriacea, costa conspicua, nervis lateralibus irregularibus, arcuatis, 2–5 utrinque supra inconspicuis subtus evidentibus siccantibus, pari basali oppositi, petiolis rectis, gracilis, angulatis siccantibus; flores bracteolis anguste ovatis subtentis. Flores fructusque evoluti non visi.

TYPE: PANAMA. COCLÉ PROVINCE: continental divide on road to Coclesito, 1600 ft, *Hammel 7205* (MO).

Tree 15–20 m tall; wood soft, white; young branches with conspicuous circular leaf scars, the twigs drying slightly narrower, dark. *Leaves* ovate or elliptical, 6–8 cm long, 2.5–4 cm wide, apically short acuminate, blunt, basally rounded, glabrous, coriaceous, the costa conspicuous, the lateral nerves irregular, 2–5 on each side, arcuate, ascending, obscure above, drying evident beneath, the basal pair opposite; petioles slender, drying angled, 2–3 cm long. *Inflorescence* cymose, bracteate, mostly covered with minute grayish trichomes, the flowers subtended by small, narrowly ovate, costate, caducous bracteoles. *Flowers* with a basal cupule which completely envelopes the young developing fruit.

This species is singular in its small leaves which somewhat resemble those of *H. cubensis* Griseb. of Cuba, but in that species the leaves are much broader and the petioles much longer and more widely spaced. This is the only species of *Hernandia* known on the American mainland with such small, crowded and uniform-appearing leaves. The bracteoles in this species are much like those in other hernandias, but may be sooner caducous. The cupule at the base of the developing fruit appears to envelop the fruit to a much greater degree than in other species. How it is placed in mature fruit is unknown.

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The type locality is an area of poorly collected disappearing wet montane forest of low elevation in central Panama.

Assisted by National Science Foundation Grant DEB 79-22192.

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PECTIS LINIFOLIA (COMPOSITAE: TAGETEAE) ADDED TO THE FLORA OF PANAMA

In the treatment of *Pectis* for the *Flora of Panama,* Keil (1975) noted that the widespread *P. linifolia* L. was known to occur both to the north and to the south of Panama but had never been collected in that country. A recent collection of *P. linifolia* var. *linifolia* has added this species to the known flora of Panama: Colón: Punta Chame, *D'Arcy 10218* (MO, OS).

This taxon would key to *P. elongata* var. *oerstediana* in the *Flora of Panama* treatment. These taxa can be easily distinguished, however. *Pectis linifolia* var. *linifolia* has a pappus of stiff, reflexed smooth awns, and its herbage is not scented. *Pectis elongata* var. *oerstediana* has a pappus of slender erect scabrous bristles, and the herbage has a strong odor resembling that of lemons or stinkbugs.

Synonymy, descriptions, illustrations and a range map for *Pectis linifolia* have been published by Keil (1978).

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Keil, D. J. 1975. VI. Tageteae. *In* R. E. Woodson, Jr. & R. W. Schery and collaborators, Flora of Panama. Ann. Missouri Bot. Gard. 62: 1220–1241.

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—*David J. Keil, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, California 93407.*

Ann. Missouri Bot. Gard. 68: 225. 1981.

VALIDATION OF THE NAME *AULONEMIA PATRIAE* POHL (GRAMINEAE: BAMBUSOIDEAE)

Aulonemia patriae Pohl (1980: 68), a new species of bamboo, was described on the basis of vegetative and fruiting material from the same colony, at Alto del Roble, Costa Rica. Since the fruiting material was long past maturity, and lacked good foliage, I indicated that two specimens, one vegetative and the other fruiting, from this colony should be regarded as syntypes. This procedure seemed to me to be available under Article 7.7 of the International Code of Botanical Nomenclature (Stafleu et al., 1978). Other taxonomists, including Dr. Stafleu, feel that it is obligatory to designate one of the specimens as a holotype or lectotype, although neither one displays all of the differential characteristics of the species. I therefore designate the following specimen as the lectotype of *A. patriae* Pohl,

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following the procedure described in the Guide for the Determination of Types, 4C (Stafleu et al., 1978).

LECTOTYPE: COSTA RICA. PROV. HEREDIA: Alto del Roble, *Pohl & Gabel 13577* (ISC).

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—*Richard W. Pohl, Department of Botany, Iowa State University, Ames, Iowa 50011.*

SETARIA VARIIFOLIA (SWALLEN) DAVIDSE, A NEW COMBINATION (GRAMINEAE: PANICOIDEAE)

Panicum variifolium Swallen, Publ. Carnegie Inst. Wash. 436: 345. 1934 is a distinctive species of the Yucatán Peninsula that should be treated as a species of *Setaria. Setaria variifolia* (Swallen) Davidse, comb. nov., has a single bristle subtending the terminal spikelet on each branch and occasionally some of the lower spikelets as well. This leaves no doubt as to its generic affinity with *Setaria*. Its slender, elliptic, acuminate spikelets with the upper floret only weakly rugose suggests a close relationship with subgenus *Ptychophyllum*. However, the blades appear to be flat rather than plicate as in *Ptychophyllum*. This plus the condensed, sparingly branched, few-flowered inflorescence suggests affinity to subgenus *Paurochaetium*. Further observations, especially field studies on the form of the blades, should eventually clarify these difficulties.

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RECOGNITION OF *BRACHISTUS* (SOLANACEAE)

The genus *Brachistus* Miers was reduced to a section of *Witheringia* L'Her. by Hunziker (1969). Further consideration of this group of plants, especially with regard to the calyx, which is dentate or lobate instead of truncate and hence has quite different vasculature, has led to belief by ourselves and by Hunziker that *Brachistus* should be restored to generic rank. Support for this concept will appear in a later publication. *Brachistus*, in our view, embraces only the species listed here and not the many others mistakenly placed in the genus in the past.

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Brachistus Miers, Ann. Mag. Nat. Hist., ser. 2, 3: 262. 1849. LECTOTYPE: *B. stramonifolius* (H.B.K.) Miers, based on *Witheringia stramonifolia* H.B.K.

Pubescent trees or shrubs. Inflorescences usually many-flowered, sessile or short pedunculate. Flowers small, 5-merous; calyx 5-dentate or lobate, the lobes sometimes short; corolla 5-lobed, the lobes longer than the tube; anthers oblong, sometimes apiculate. Fruit a berry, subglobose, enclosed one-half or more by the accrescent calyx; seeds fabiform. (Adapted from Hunziker, 1969).

Brachistus stramonifolius (H.B.K.) Miers, Ann. Mag. Nat. Hist., ser. 2, 3: 263. 1849. Southern Mexico to Panama.

Brachistus nelsonii (Fern) D'Arcy, J. L. Gentry & Averett, comb. nov.

Athenaea nelsonii Fern., Proc. Amer. Acad. Arts 35: 567. 1900. TYPE: Mexico, Chiapas, *Nelson 3395* (GH, holotype; US, isotype). Southern Mexico to Panama.

Brachistus affinis (Morton) D'Arcy, J. L. Gentry & Averett, comb. nov.

Athenaea affinis Morton, Contr. Univ. Mich. Herb. 4: 24. 1940. TYPE: Belize, *Lundell 6452* (US, holotype; A, F, US, isotypes). Belize.

KEY TO SPECIES

a. Leaves acute or obtuse to nearly truncate at the base .... *B. stramonifolius*
aa. Leaves cordate at the base.
- b. Pubescence of long, glandular hairs, at least some of the hairs 1 mm long; corolla marked with purple .... *B. nelsonii*
- bb. Pubescence of short, eglandular hairs, the hairs less than 1 mm long; corolla not marked with purple .... *B. affinis*

LITERATURE CITED

HUNZIKER, A. T. 1969. Estudios sobre *Solanaceae* V. Contribucion al conocimiento de *Capsicum* y generos afines (*Witheringia, Acnistus, Athenaea*, etc.) Kurtziana 5: 101–179.

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1982 AETFAT CONGRESS

The 1982 AETFAT Congress will take place from 19–22 January 1982 at the CSIR Conference Centre, Pretoria, Republic of South Africa. The congress is organized by the Botanical Research Institute of the Department of Agriculture and Fisheries, Secretariat of the "Association pour l'Etude Taxonomique de la Flora d'Afrique Tropicale" (AETFAT) and the "South African Association of

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Botanists" (SAAB), assisted by the Symposium Secretariat of the "Council for Scientific and Industrial Research" (CSIR).

A symposium on "The Origin, Evolution and Migrations of African Floras" will be a major feature of the congress. The aims of this symposium are to supply a brief overview of the present state of knowledge on the evolution of African floras and vegetation, particularly in the light of the movements of continents and of climatic changes: to link these facts with the distribution, composition and diversity of present-day floras and vegetation in an attempt to unravel their past history. Whereas only the more recent fossil deposits have a strong bearing on present-day floras, the accounts on older deposits are being deliberately included to be able to present as complete a picture as possible, and to reflect current research activity in this field.

A number of the topics included in the proposed symposium were discussed during the Symposium held at the Missouri Botanical Garden in 1977 on the phytogeography of Africa. The proceedings of this symposium were published in the ANNALS OF THE MISSOURI BOTANICAL GARDEN Vol. 65: 367–589 (1978) and have stimulated general interest. It is felt that these topics could well be approached from a more regional point of view in 1982 so that more detailed information will become available for many of the African countries.

All inquiries concerning the congress should be addressed to: The Symposium Secretariat S.229, CSIR, P.O. Box 395, Pretoria 0001, South Africa. Telephone: International + 27 12 86-9211, extension 2077 (Elsie Coetzee) or 2063 (Ann van Dyk). Telex: SA 3-630.

FLORA MESOAMERICANA

The Missouri Botanical Garden, the Instituto de Biología of the Universidad Nacional Autónoma de México and the British Museum (Natural History) are collaborating to produce a synoptic Flora of the estimated 16,000 vascular plants of Mesoamerica. This Flora will serve as a concise identification manual of Mesoamerican plants.

Such a project has been discussed in the botanical community for many years and is of such a magnitude that it would, if it were to be successful, require the cooperation of many institutions within Mesoamerica and outside of it. With this basic premise the three organizing institutions began discussions for a Flora Mesoamericana Project in 1979 and appointed G. Davidse (MBG), M. Sousa (UNAM), A. O. Chater (BM) and J. C. Humphries (BM) as organizers and editors of this project. From these initial discussions a plan of action was developed. In early 1980 a broad outline of the plan of action was distributed to individuals and institutions from Mesoamerica, the U.S. and Europe historically active in Mesoamerican botanical studies. Comments were solicited and invitations were extended to attend an organizational and planning meeting sponsored by the three organizing institutions in St. Louis, 14–15 July 1980. Twenty-five persons representing 13 institutions attended: British Museum

(Natural History), California Academy of Sciences, Colegio Superior de Agricultura Tropical, Duke University, Field Museum of Natural History, Herbario Nacional de Colombia, Herbario Nacional de Nicaragua, Instituto Politécnico Nacional, Missouri Botanical Garden, National Science Foundation, Universidad Nacional Autónoma de Honduras, Universidad Nacional Autónoma de México and Universidad de Panamá. General approval and support were given to the need for such a project and wide agreement was reached on matters of procedure.

The Flora will be published in Spanish by the Universidad Nacional Autónoma de México and will appear in seven volumes over a period of sixteen years. As much of the Flora as possible will be written by experts, the remainder by staff of the organizing institutions. It will summarize existing information and incorporate much new research. Keys and descriptions will be included at all levels. Types and selected specimens will be cited, and sufficient synonymy will be given to correlate the Flora with previously published work in the area. A concise statement about distribution and ecology will also be included. In general the style of the Flora will be very similar to that of *Flora Europaea*.

The area to be covered by the *Flora Mesoamericana* will include Panamá, the Central American republics, the Yucatán Peninsula and Chiapas. Where to draw the exact boundaries for the Flora was largely pragmatic. Having the Panamanian-Colombian frontier serve as the southern boundary seems to be logically dictated on a geographical basis. In addition, since the *Flora of Panama* ends at that border and since the new *Flora de Colombia* project will adequately cover the area east of this border, this boundary seems to be a logical one. The northern boundary clearly should be in the Isthmus of Tehuantepec region. A very good phytogeographical one seems to be following (M. Sousa and D. Breedlove, pers. comm.): from the Gulf of Tehuantepec along the Tehuantepec River, to the Sierra Mixe to the 300 m contour, west along the Sierra Mixe and the Sierra de Juárez to the Papaloapan River, and along this river to the Gulf of México. However, it was strongly and unanimously agreed at the St. Louis meeting that such a boundary would be highly impractical for specimen handling and distribution plotting and that using the Veracruz-Oaxaca and Tabasco-Chiapas borders would at once be practical for specimen handling and at the same time include virtually all of truly tropical México. It was realized that a case could well be made for extending the northern boundary into Veracruz and perhaps into Tamaulipas. However, a significant number of basically northern species would then be included (Rzedowski, pers. comm.). Thus a practical political boundary was chosen with the provision that for taxa extending just beyond this boundary and which seem to have a truly southern tropical derivation, authors could decide to include these taxa in the Flora on a case-by-case basis.

A concurrent collecting program has been started by the three organizing institutions in conjunction with other botanists and institutions in Mesoamerica. It is aimed at significantly strengthening current attempts to collect in poorly or never-collected areas before the surviving natural vegetation is completely destroyed. A knowledge of these areas is necessary for comprehensive coverage

in the Flora. Specialist collecting by persons contributing family treatments is also scheduled to the extent possible by available funds.

When completed, the Flora will comprise a data base for the floristics and taxonomy of the area. From such a firm taxonomic framework it will be possible to plan more effectively detailed taxonomic studies in the area, as well as broader programs in conservation and land use. Additionally, we foresee that the production of local and special purpose floras of individual countries or areas and covering such topics as economic and medicinal uses will be a major spin-off from the *Flora Mesoamericana*.

The organizers and editors welcome inquiries and correspondence concerning any aspect of the project—Gerrit Davidse (Organizer and Editor), Missouri Botanical Garden, P.O.B. 299, St. Louis, MO 63166, U.S.A.; Mario Sousa (Organizer and Editor). Instituto de Biología, Herbario Nacional, U.N.A.M., Apartado Postal 70-367, México 20, D.F., México; C. J. Humphries (Organizer), and A. O. Chater (Editor), Botany Department, British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.

THE 1981 JESSE M. GREENMAN AWARD

The 1981 Jesse M. Greenman Award has been won by William R. Buck for his publication "A Generic Revision of the Entodontaceae" (J. Hattori Bot. Lab. 48: 71–159. 1980.). This monographic study is based on a Ph.D. dissertation from the Department of Botany, University of Michigan, Ann Arbor.

The Greenman Award, a cash prize of $250, is presented each year by the Alumni Association of the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation which was published during the *previous* year. Papers published during *1981* are now being considered for the 15th annual award, which will be presented in the summer of 1982. Reprints of such papers should be sent to: Greenman Award Committee, Department of Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166, U.S.A. In order to be considered for the 1982 award, reprints must be received by 1 July 1982.

ANN. MISSOURI BOT. GARD. 68: 230. 1981.

ERRATA

Thorp, Robbin W. 1979. Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. Ann. Missouri Bot. Gard. 66: 788–812.

P. 791, in Table 1, should read Hylaeinae, not Hyaelinae.

P. 797, Fig. 12 caption, should read *Paratetrapedia (Paratetrapedia)* not *Exomalopsis*.

P. 809, Grinfeld, E. K. should read 1962, vol. 41 not 1969, vol. 48.

P. 811, Pasteels, J. M. & J. J. Pasteels should read 1977, Arch. Biol. 88: 441–468, not 1979 (in press).

P. 811, Thorp, R. W. & D. L. Briggs should read 1980, 53: 166–170, not 1979 (in press).

I thank J. Neff, Austin, Texas, for bringing the first errors to my attention.

—*Robbin W. Thorp, Department of Entomology, University of California, Davis, California 95615.*

ANN. MISSOURI BOT. GARD. 68: 231. 1981.

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 67, No. 4, pp. 819–1069, was published on 29 June 1981.

Index to plant chromosome numbers 1975—1978

Chromosomal information has become increasingly important in recent years in studies of plant systematics and evolution. Nearly all modern taxonomic monographs and revisions include chromosomal data and use this information in analyzing species or generic relationships or evolutionary patterns.

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DISPERSAL VERSUS GENE FLOW IN PLANTS[1]

DONALD A. LEVIN[2]

ABSTRACT

The notions that gene flow in plants is restricted and that neighborhood size and area are small are based upon data on pollination, and pollen and seed dispersal. However, neighborhood size and area estimates from these data incorporate several assumptions: (1) Pollinator flight distance is representative of pollen dispersal distance; (2) All pollen picked up by pollinators from one plant is deposited on the next one visited; (3) Pollinator flights between plants are random in direction; (4) Pollen-pistil compatibility is independent of the proximity of egg and pollen parents; (5) Seed viability is independent of the proximity of egg and pollen parents; (6) Seed production is independent of the proximity of seeds to the source; (7) The fitness of plants is independent of the distance between egg and pollen parent. These assumptions have been found to be unwarranted in many instances leading to the following conclusions: (1) Pollen carry-over may be considerable; (2) Pollinator flight sequences have a directional component; (3) Pollen-pistil compatibility may be lower among near-neighbors than among moderately spaced plants; (4) Seed abortion may be higher following self and near-neighbor crosses than following wide crosses; (5) Seed-set may be lower following crosses of neighboring plants than widely spaced plants; (6) Seed and seedling mortality may increase as the seed source is approached; (7) Fitness of offspring from distant crosses may be superior to that from self or near-neighbor crosses; (8) Gene flow over some distance may be higher in natural populations than in crops. There is abundant reason to believe that dispersal data underestimate gene flow. As a consequence, we may conclude that neighborhood sizes and areas are larger, there is less potential for random differentiation, there is less isolation by distance, there is less potential for geographical differentiation, and that stronger selection is needed to foster and maintain local differences than judged from dispersal data alone. Nevertheless, even if gene flow distances were twice as large as we now think, the spatial scale of gene dispersal: (1) is still small enough to allow substantial differentiation over short distances with moderate selective differentials, and (2) is too small to be a major cohesive force within a species.

In 1969, Ehrlich & Raven challenged the prevailing view that plant species were Mendelian populations integrated by gene flow. They argued that gene flow probably is much too restricted to homogenize anything but local gene pools. They pointed to selection as the primary cohesive and disruptive force in evolution. Selection would determine the influence of gene flow, often counterbalancing it in the course and maintenance of microgeographic differentiation.

[1] This study was supported in part by National Science Foundation Grant DEB 78-23654. I am indebted to John Endler and Verne Grant for suggesting several ways to improve the paper.
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The general model of restricted gene flow has received substantial support from the crop and native plant literature on pollinator foraging behavior, and pollen and seed dispersal (Levin & Kerster, 1974; Levin, 1979). For the most part, pollinators fly from a plant to one of its near neighbors, suggesting that cross-pollinations are principally between neighboring plants. Animal- and wind-borne pollen dispersal tends to assume a leptokurtic distribution, with most pollen being deposited within a few meters of the source. In most species, pollen is rarely transported beyond 1000 m. Seeds also tend to be distributed narrowly about the source and are rarely carried beyond 200 m.

Data from pollinator foraging behavior, and pollen and seed dispersal may be incorporated into population genetic models to obtain a first approximation of the breeding structure of populations (Levin & Kerster, 1974). In the process, a number of simplifying assumptions typically are made. These are as follows: (1) pollen picked up by a pollinator is deposited on the next plant visited; (2) pollinator flights between plants is random in direction; (3) pollen-pistil compatibility, seed viability and seed-set are independent of pollen to egg parent distances; (4) seed and seedling survivorship are independent of the proximity to the seed source; (5) populations have no seed pool; (6) interpopulation gene flow is independent of population size and patterns of plant distribution.

The major purpose of this paper is to test these assumptions. I will show that dispersal data underestimate the expanse of gene flow, but that the breeding structure of populations is still sufficiently restricted in space to permit selective differentiation over short distances.

Pollinator Foraging Behavior and Pollen Flow

Pollen flow distances would be distributed as pollinator flight distances were all pollen collected from one plant deposited on the next visited by a pollinator. Given the inefficiency of the pollen transport mechanism, it seems likely that there would be carry-over to a second, third or fourth plant. Thomson & Plowright (1980) were able to assess the functional form and extent of pollen carry-over in the bumblebee-pollinated *Erythronium americanum* by introducing a single red-pollen flower into a bees foraging sequence, and examining successively visited yellow-pollen flowers. Pollen usually was deposited on 7 or more flowers. In one sequence, pollen was deposited on several flowers through the 20th and then on numbers 23, 25, 29, and 54. In most sequences maximum pollen loads were deposited on the second flower or subsequent ones; and the deposition schedule was platykurtic. Thomson & Plowright also analyzed carry-over in bumblebee-pollinated *Clintonia borealis* and *Diervilla lonicera* using emasculated flowers. Pollen usually was carried beyond the fifth flower (often to the eighth). In many runs the initial fall-off of pollen loads roughly approaches a negative exponential function.

Before considering the extent to which pollen carry-over increases the distance pollen is transported, it is necessary to consider whether pollinators forage at random with regard to direction in successive flights. Zimmerman (1979) argued that in a population where the probability of revisiting any specific flower was small, pollinators should forage at random with regard to the direction of successive moves; i.e., angles of departures should have a uniform distribution. He

TABLE 1. Pollen dispersal as influenced by pollen carry-over and flight directionality.

Carry-over Schedule	Direction Constant[a]		
	D = 0	D = 0.71	D = 1
A. I[b] = 50%, II = 20%, III = 15%, IV = 10%, V = 5%	1.35	1.57	2.00
B. I = 40%, II = 10%, III = 10%, IV = 10%, V = 10%, VI = 10%, VII = 10%	1.74	2.12	3.10
C. I = 20%, II = 10%, III = 20%, IV = 10%, V = 20%, VI = 10%, VII = 10%	1.84	2.45	3.70
D. I = 20%, III = 20%, V = 20%, VII = 10%, IX = 10%, XI = 10%, XIII = 10%	2.25	3.30	5.80
E. I = 50%, V = 20%, X = 10%, XII = 10%, XX = 10%	1.59	3.67	6.00

[a] Direction Constant × Mean Flight Distance = Mean Pollen Dispersal Distance; D = 0 refers to random flights; D = 1 unidirectional flights; D = 0.71 observed directionality.

[b] Roman numerals refer to plant number in a sequence.

observed that the bumblebee *Bombus flavifrons* forages randomly with respect to direction on *Polemonium foliosissimum*. Likewise, Gill & Wolf (1977) reported that the departure direction for sunbirds (*Nectarinia* sp.) feeding on *Leonotis nepetifolia* was usually independent of the arrival direction. On the other hand, strong directional components to pollinator foraging have been reported in the case of *Bombus* sp. working *Aconitum columbianum* and *Delphinium nelsonii* (Pyke, 1978), *Bombus* on *Armeria maritima* and *Limonium vulgare* (Woodell, 1978), sweatbees (Halictidae) on *Convolvulus arvensis* (Waddington, 1979), various bees and butterflies on *Lythrum salicaria* (Levin et al., 1971), and *Apis mellifera* on artificial flowers (Waddington, 1980). A correlation in the direction of successive flights increases the distance pollen is carried, if there is pollen carry-over.

The specific effects of pollen carry-over and directionality on pollen dispersal are best described with a series of simple models. Consider first a case of pollen carry-over with no directional component to foraging. The mean pollen dispersal distance with carry-over equals the flight mean × [Σ proportion pollen deposited on the ith plant × $\sqrt{i}$] (Levin et al., 1971); i^{th} plant in a random foraging bout is (on the average) $\sqrt{i}$ plants from the pollen source. The extent to which carry-over increases pollen dispersal beyond pollinator flight moves is shown in Table 1. The percentage increase is dependent on the carry-over schedule, the more liberal the schedule the larger the effect. Note that regardless of the schedule, carry-over increases the mean pollen dispersal distance several percent.

The effect of directionality of pollen dispersal distance is most easily demonstrated if we assume that pollinators fly in a straight line. With random pollination, the ith plant is ($i^{0.5}$) × (mean flight distance) from the location of the pollen donor. With all flights in the same direction, the exponent of the ith plant is 1, so that the ith plant is (i^1) × (mean flight distance) from the pollen source. The mean pollen dispersal distance with unidirectionality is the (mean pollinator flight distance) × (Σ proportion of pollen deposited on the ith plant × i^1). Let us assume that 50% of the pollen from a plant is deposited on the first plant, 20% on the second, 15% on the third, 10% on the fourth, and 5% on the fifth plant visited. The mean dispersal distance with this carry-over schedule is twice that of the

mean flight distance. With random foraging, the dispersal mean is 35% greater than the flight mean. The effect of directionality when combined with other carry-over schedules is summarized in Table 1.

Having considered the consequences of carry-over within the context of no directionality and complete directionality, let us turn to a more realistic scenario, one involving moderate directionality as observed in natural populations. With a positive correlation in arrival and departure directions, the mean distance of the ith plant from the pollen source is between $i^{0.5}$ and $1^1 \times$ (mean flight distance), the exponent increasing as the correlation increases (Levin et al., 1971). The exponents based on field observations vary from 0.69 and 0.72 for honeybees and butterflies, respectively, on *Lythrum salicaria* (Levin et al., 1971) to 0.85 for bumblebees on *Aconitum* and *Delphinium* (Pyke, 1978). Using 0.71 as a representative exponent, I calculated the effect of moderate directionality coupled with various carry-over schedules on pollen dispersal. The results are presented in Table 1. The mean pollen dispersal distance is increased by a factor of 1.5 to more than 3. Thus pollen may move substantially farther than we would surmise from pollinator foraging data. Carry-over and directionality open the breeding structure of populations.

Thus far we have seen evidence for and consequences of pollen carry-over and flight directionality. It is important to recognize that neither carry-over schedules nor the magnitude of directionality are fixed attributes of a plant-pollinator relationship. Rather, both are dependent on the amount of floral reward; and this has some interesting implications for pollen dispersal. As noted earlier, Thomson & Plowright (1980) documented carry-over schedules by analyzing pollen deposition levels in relation to the number of pollinator moves from the pollen source. In addition to employing unmanipulated flowers, they provided bees alternately with nectar-enriched and nectar-drained flowers of *Diervilla lonicera*. Taking run and sequence position into account, enriched flowers received significantly more pollen than drained ones. Pollen deposition per flower, or more precisely the fraction of the load deposited, is a simple function of the time spent on the two flower types; significantly more time is spent on enriched flowers. Heinrich (1979b) also studied the relationship between time and floral reward. He analyzed foraging behavior of *Bombus terricola* workers in a field of *Trifolium repens* in which sectors had been screened for two days to exclude foragers. On the average, bees foraging in the rich clover patches visited 2.95 heads per minute compared to 18.9 heads per minute in the depleted clover patches. Bees in the rich clover probed into 11.6 florets/head, vs. 2.3 florets/head in the depleted clover. It is likely that much more pollen was deposited per head in the rich patches than in the depleted ones. Correlatively, there was probably much less carry-over in the rich patches.

Bees also modify their directionality in response to resource quality. Pyke (1978) showed that the mean angular deviations of *Bombus* arrivals and departures on inflorescences of *Aconitum columbianum* and *Delphinium nelsonii* increased as the number of flowers visited per inflorescence increases. Thus as nectar reward per inflorescence increases, there is less correlation between successive flights, and pollinators will tend to stay in an area. Heinrich (1979b) monitored the angular deviation of *Bombus* on successively visited clover heads

in rich and depleted patches. In the rich patches bees had high angular deviations, whereas bees tended to pass through patches where resources per flower were low. This aspect of foraging behavior is consistent with that described for predators feeding on prey (cf. Pyke et al., 1977).

It is possible that directionality may vary as a function of plant density. Pollinators might move more directly and rapidly through a population if the energy gain : expenditure ratio were relatively low because of large interplant distances. If pollinators are found to move with greater directionality as density declines, this behavior would compound the effect of low density on flight distance and thus on pollen flow. The lower the density the greater is the mean flight distance (Levin & Kerster, 1974). If a sparse population also had small plants, then the level of directionality and flight distance would be high, and jointly result in unusually (for the species) broad pollen dispersal.

Bee flight distance as well as directionality varies with resource qualty. In the case of *Bombus flavifrons* workers on *Aconitum columbianum*, the mean distance moved by bees from one inflorescence to another decreases toward an asymptote as the number of flowers on an inflorescence increases (Pyke, 1978). Pyke regards the numbers of flowers visited per inflorescence as an indicator of resource quality, so that as quality declines flight distance increases. *Bombus terricola* foraging on *Trifolium repens* displays the same general behavior. The distances of inter-head moves in depleted patches was approximately twice that in rich patch, i.e., patches that were screened for two days (Heinrich, 1979a). On the average, bees foraging in the depleted patches rejected (without landing or probing) 27% of the flower heads they approached. When they entered rich patches, they rarely (0.4%) rejected heads they approached.

The foraging movements (viz. directionality and distance) described by Pyke (1978) and Heinrich (1979b) follow patterns predicted by mathematical models based on optimal foraging. Accordingly, we would expect other types of bees and indeed other categories of pollinators to forage in a similar manner. Given that pollinators respond to resource quality as the *Bombus* species, pollen flow will be considerably greater in depauperate populations than in rich ones. Since this condition will most likely vary through time, the same population may be both depauperate and rich, and correlatively have different pollen dispersal profiles over time. When nectar levels are very low due to temperature or moisture stress (Percival, 1965), pollen flow may be relatively broad for a considerable period.

If pollinators respond to single flowers or inflorescences in predictable ways, they probably would also respond to the entire plant in the same ways, were the sum of the open flowers at some time the measure of quality. If site quality is poor, plants would produce few flowers per unit time, and have relatively few open flowers at any one time. A pollinator may "treat" this population as nutritionally depauperate because the energy gain per plant is small, and as a consequence move farther and in a more directional manner than if the plants had numerous flowers. Accordingly, pollen dispersal would be more widespread than usual in a marginal site. On the other hand site quality may be unusually good, and plants may be unusually florificent. Then pollen flow might be more restricted than usual.

The discussion thus far has considered only pollination of single plant species.

However, pollinators are not completely flower constant in natural communities. There is usually some switching of species by lepidopterans, hummingbirds, bumblebees, and to a lesser extent by honeybees (Baker & Hurd, 1968; Free, 1970; Proctor & Yeo, 1973). Individual bumblebees typically major on plant species and minor on one or a few others (Heinrich, 1976, 1979a). A minor species may differ manifestly from the major in its floral architecture and correlatively have its pollen transported in a position different from that of the major. Accordingly, pollen from a minor plant is apt to be transported to other minor plants even though several majors may intervene. Even if floral structures were similar, some pollen of the minor probably would be transported to another minor. By virtue of the fact that minor plants only intermittently are visited, cross-pollination among them often will be between widely spaced conspecifics, the distances being much larger than if the species were a major. Carry-over of minor pollen would augment the effect. Thus by virtue of being treated as a minor, the breeding structure of a species may be substantially enlarged. A given plant species may not be treated as a minor by all bees in a population. In that case, the pollen dispersal profile will be a composite of a typical leptokurtic distribution and a collection of relatively long distance events residing in the tail of that distribution.

Potential Versus Actual Gene Flow

Whereas the foraging behavior of pollinators suggests where pollen may be transported, the actual dispersal of pollen and hence pollen-mediated gene flow may be determined by the dispersion of genetic markers relative to a central point in a population. If we introduce a homozygous dominant genetic marker into a population, allow pollen to be dispersed, collect seed at various distances from the source, and determine the percentage hybrid plants as a function of distance, we would have a reasonably accurate measure of gene flow in that population. If we observed pollinator flight distances from the marker, we would then be able to compare flight and gene flow distances. Were all pollen deposited on the first plant visited, then pollinator flight and gene flow distributions would be concordant. Pollen carry-over would result in the divergence of the two distributions, the greater the carry-over the more discordant the distributions.

In 1973 I began an investigation of gene flow in natural populations of *Phlox drummondii*, a spring-flowering annual of central Texas. I introduced a core of ca. 100 plants of a cultivar (Twinkle) into an extensive population near Gonzales, Texas. The cultivar was homozygous for a dominant corolla lobe character. Seeds were collected every two days in 1 m wide concentric rings around the core, and were progeny tested in the greenhouse. The principal pollinator of *P. drummondii* was *Battus philinor*. This and other lepidopterans were scored for interplant flight distance. Data for three episodes of pollination and gene flow are presented in Figure 1. Each pollination episode was scored over several days 3 to 4 weeks prior to each seed collection. Since the seeds mature in 3 to 4 weeks, the amount and distribution of hybrids will be a function of the foraging behavior we observed. The pollinator flight distribution was highly leptokurtic, with most flights being 2 m or less. A small percentage of the flights exceeded 10 m (Fig. 1). The mean flight distance was ca. 2.75 m. In contrast, the gene flow pattern was less leptokurtic, and had more events beyond 10 m. Mean gene flow

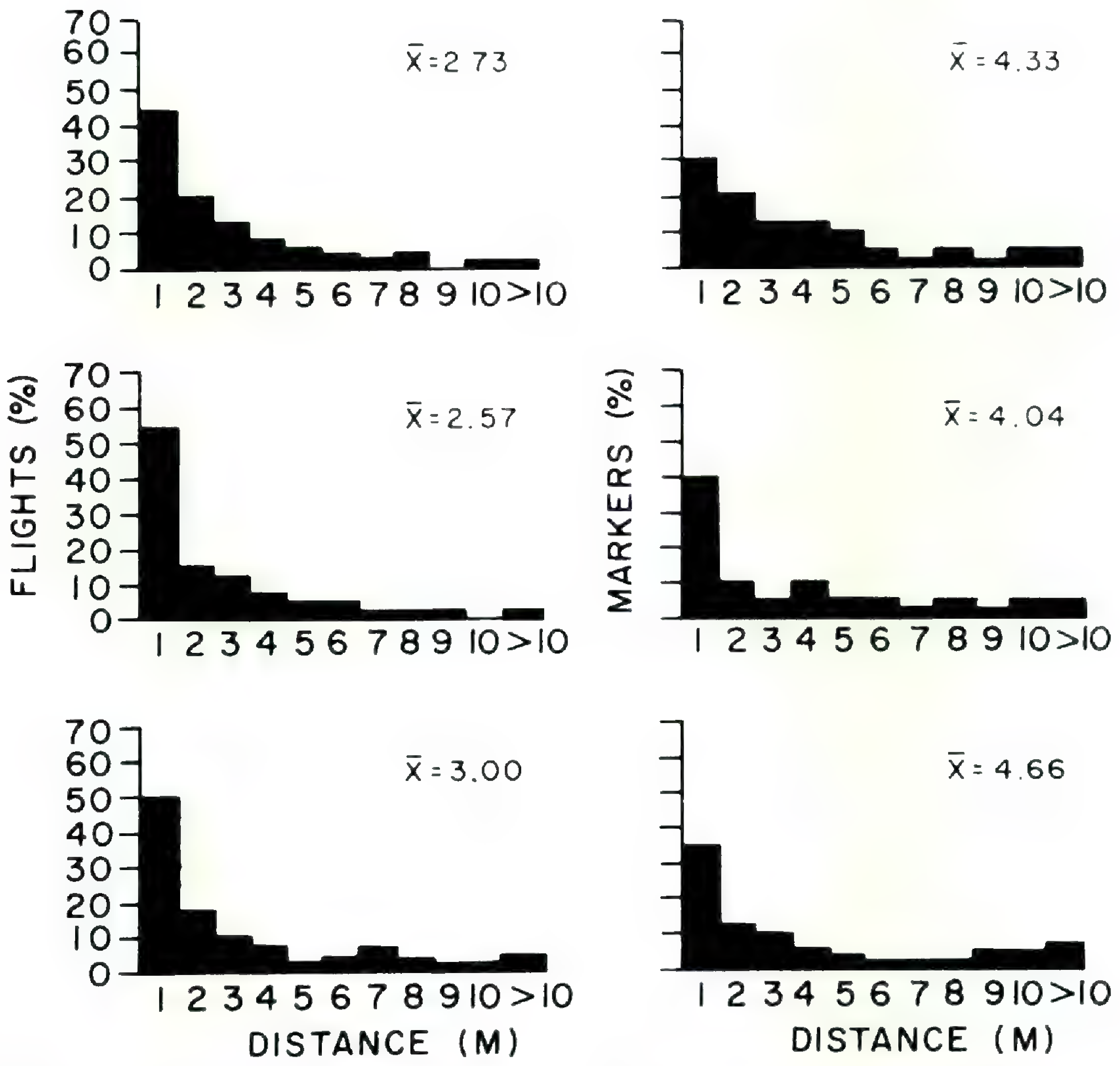

FIGURE 1. Pollinator flight distance and gene flow distance at three periods of the growing season in a population of *Phlox drummondii* (Gonzales, Texas).

distance was about 4.3 m, which was about 1.5 times the mean flight distance. This difference must be due to pollen carry-over.

A disparity between pollinator flight and gene flow distributions also has been observed in *Lupinus texensis* by Schaal (1980). She placed 7 plants homozygous for an electrophoretic marker into a synthetic population of 91 plants lacking this marker. Bees were allowed to forage for 3 days and their flight distances were scored. Thereafter all plants were returned to the greenhouse, and seeds were collected subsequently from the field bee-exposed flowers. Mean pollinator flight distance was 0.97 m vs. 1.82 m for the gene flow distance. The level of kurtosis was significantly higher in the flight distribution. The differences in means and kurtosis are the result of pollen carry-over.

Differential Crossability

It is tempting to assume that parental distances are distributed as are the distances of pollen grains. However, pollen grains from all plants do not have an equal probability of effecting fertilization in a given plant. The self-incompatibility (S) locus may preclude certain types of crosses. Pollen which shares a self-compatibility allele with another plant is excluded from breeding with it (de Nettan-

court, 1977). Given the richness of S-alleles in natural populations, plants sharing S-alleles are likely to be related. This means that in populations where seed dispersal is highly restricted, and thus where neighboring plants are often related, a distant pollen grain is more likely to effect fertilization than a pollen grain from a neighboring plant.

The success of pollen, or its fertilization ability, may be a function of the similarity of the pollen genotype to the stigma genotype. Pfahler (1965) analyzed the fertilization ability of maize pollen using pollen mixtures containing 50% pollen from each of two parents. The two pollen types are equally successful if 50% of the progeny have a marker from one parent. When pollen from a source related to the female was mixed with pollen from unrelated sources in various 2-way combinations, between 33% and 43% of the fertilizations involved the related pollen. Thus related pollen was at a disadvantage, and negative assortative mating ensued. Since self-pollen often is competitively inferior to outcross pollen in mixtures (cf. Mulcahy, 1975), it is likely that the disadvantage of related outcross pollen vis-à-vis unrelated pollen is a common phenomenon.

Given that pollen-pistil compatibility might vary with relatedness, might it also vary with distance in species with narrow seed and pollen dispersal? We sought the relationship between pollen-pistil compatibility and plant distance in *Phlox drummondii*. Pollen and seed dispersal in this species typically is a few meters or less, and populations display significant heterozygote deficiency relative to Hardy-Weinberg expectations (Levin, 1977). These observations suggest that populations undergo moderate inbreeding.

Phloxes were collected as seedlings along 35 m linear transects in each of 14 populations. The seedlings were grown to maturity in the greenhouse. Crosses were made within and between populations. Crossability was considered in terms of the spatial relationships of the pollen and egg parents which were known. On the average, pollen grain germination increased with distance up to 10 m. Additional distances up to 35 m were not accompanied by overall changes in germination percentage. Pollen germination averaged about 17% with near-neighbor pollinations vs. ca. 20% with pollinations involving plants 10 m away or more. Pollen from parents in neighboring populations displayed germination rates similar to those found in intrapopulation crosses beyond 10 m. Pollen from sources greater than 20 km away performed substantially below that of pollen from within populations or from neighboring populations, mean germination being ca. 19% and 14%, respectively. Thus pollen germination rates are highest when mating plants are moderate distances apart.

The crossability of two plants depends not only on pollen-pistil compatibility, but also upon the vigor of the developing seed. The developing seed is sensitive to genetic disharmonies brought about by inbreeding. High levels of seed abortion following inbreeding are well known in numerous predominantly outcrossing species (Crumpacker, 1967; Franklin, 1970).

Of particular interest within the context of this discussion is whether abortion is dependent on the distance between mating plants. If relatedness is a function of distance, we would expect abortion levels between neighboring plants to be higher than that between plants several meters apart. In populations of *Phlox drummondii*, seed abortion decreased with interparent distances up to about 10

m, and remained at that level as distances increased to 35 m. Abortion following crosses of 1 m or less averaged 18% vs. 14% following crosses of 10 m and more. It seems likely that higher abortion in the progeny of crosses between neighbors reflects their overall relatedness, because abortion levels increase substantially with self-fertilization. Crosses between neighboring populations did not yield lower abortion levels than that observed at interparent distances beyond 10 m within populations. Crosses between populations more than 20 km apart did yield significantly higher abortion rates (19% vs. 14%). Distance-dependent abortion rates also have been described within *Picea glauca* (Coles & Fowler, 1976). Crosses between plants less than 100 m apart yielded 28% less sound seed than crosses at greater distances. Selfing produces little sound seed. Presumably some plants near each other were relatives, so that inbreeding varied as a function of distance.

Seed-set in plants is dependent upon pollen-pistil compatibility and seed viability. In *Phlox drummondii,* seed-set tends to increase as the distance between plants within a population increases. This pattern is evident across populations. Seed-set from crosses between near neighbors averages 53% compared to 65% for crosses between plants at least 10 m apart. Crosses between neighboring populations have seed-sets similar to that of crosses between plants 20 m apart ($\bar{x}$ = 63%). However, crosses between populations more than 20 km apart yielded lower seed-set ($\bar{x}$ = 55%) than crosses between neighboring populations. Thus the general pattern is one of an intermediate optimum, more than a few meters and less than 20 km.

Seed-set following crosses between parents separated by various distances has also been analyzed in *Delphinium nelsonii* (Price & Waser, 1979). For the most part, 10 m crosses gave higher seed-set in the two study populations over two years than crosses over 1 m, 3 m, 30 m, 100 m and 1000 m. The pattern of an intermediate optimum also has been described in *Stylidium.* In *S. elongatum* and *S. confluens,* the percentage seed-set was greater in crosses separated by 40 to 60 km than in crosses of smaller or greater distances (Banyard & James, 1979). Since embryo abortion often follows self-fertilization in these species, it seems likely that reduced seed-sets in intrapopulation crosses were a manifestation of inbreeding depression. A decline in seed-set between "distant" populations in *Delphinium* and *Stylidium* may be due to genome incompatibility fostered by divergent local adaptations.

As we study fine scale crossing relationships in natural populations, it is evident that the facility with which plants interbreed is dependent on their spatial relationships which are correlated with their genetic relationships. On the average, neighboring plants in outcrossing species seem less likely to successfully interbreed than plants tens to hundreds of meters apart. As a consequence, the breeding structure of populations may be more open than we would imagine.

Differential Viability

The breeding structure of populations needs to be considered in terms of the resulting standing crop as well as the zygote or seed population. As the breeding structure of the seed population is shaped by genotype-dependent mortality during development, so the breeding structure of the adult population is shaped by

genotype-dependent mortality throughout the vegetative phase of the life cycle. In essence, there is a potential and realized breeding structure. The former describes the mating pattern, the latter integrates the mating pattern and mortality.

Products of outcrossing typically have higher viability than products of selfing during seed development and as established plants (Allard et al., 1968; Stern & Roche, 1974; Janossy & Lupton, 1976). In conifers the incidence of seed abortion (Koski, 1971, 1973; Birshir & Pepper, 1978), and defective or slow growing seedlings (Franklin, 1970; Koski, 1973) is 2 to 5 times higher with selfing than with outcrossing. The genetic load per zygote averages more than 8 lethal equivalents in some species of *Pinus* and *Pseudotsuga* (Franklin, 1972; Sorensen, 1969; Koski, 1973). Although zygote populations of many species are often somewhat inbred, the level may diminish through time as a result of differential mortality. For example, in *Eucalyptus pauciflora* the average outcrossing rate for seeds is 63% compared to 76% for seedlings (Phillips & Brown, 1977). Different outcrossing rates are seen even among seeds stored for different periods. In *Eucalyptus delegatus*, outcrossing rates in old seeds was 85% versus 66% in the most recent collection (Moran & Brown, 1980).

Differences in seedling quality as a function of interplant distances have been found when sought. One component of seedling quality, epicotyl length was studied in the progeny of crosses of various distances in *Picea glauca*. Epicotyls of progeny of near-neighbor crosses were shorter than those from distantly spaced parents (Coles & Fowler, 1976). These data suggest that neighboring plants were related, especially since the epicotyls of self-pollinated seedlings were 24% shorter than those from long-distance outcrosses. Differences in epicotyl length as a function of distance have obvious fitness implications in that the larger seedlings within a cohort usually have higher survivorship than the smaller ones (Harper, 1977).

The effects of interparent distance on seedling survivorship have been described in *Delphinium nelsonii* (Price & Waser, 1979). Seedlings from crosses between plants 10 m apart had higher survivorship in the native sites than seedlings from crosses between plants 1 m, 100 m, and 1000 m apart, respectively. Self-seedlings had the lowest survivorship. Price & Waser conclude that seedlings from crosses between neighboring plants may be suffering inbreeding depression, whereas the seedlings of wide crosses may be suffering genomic incompatibility.

Survivorship within a cohort is most likely to be genotype-dependent with mixed selfing and outcrossing. In species of inbreeding annuals, it is common to find an excess of heterozygotes relative to expectations based on the mating system (Allard et al., 1968; Clegg et al., 1978). Comparisons of seedlings and adult genotypes from natural populations of *Avena barbata* showed that heterozygotes at one of 3 esterase loci had about a 30% advantage over the homozygotes (Clegg & Allard, 1973). In *Avena sativa*, heterozygotes for two loci governing crown rust reaction had a 50% advantage over homozygotes (Fatunla & Frey, 1980). On the other hand, no substantial viability advantage was found in single or multilocus heterozygotes in experimental barley populations (Clegg et al., 1978). Genotype frequencies in parents and progeny have been analyzed in *Eucalyptus pauciflora* (Phillips & Brown, 1977) and *E. delegatensis* (Moran &

Brown, 1980). Heterozygotes appear to have about a 20% advantage in the former, and a 50% advantage in the latter. In perennials changes in heterozygosity through time may be inferred from genotype frequencies in different age classes all sampled at one time. Using this approach, Schaal & Levin (1976) found a substantial increase in heterozygosity through time in *Liatris cylindracea*. Differential survivorship in favor of heterozygotes effectively opens the realized breeding structure of populations because survivors are weighted in favor of the progeny of unrelated plants.

Seed Dispersal

Distributions of seed dispersal distances have been described for numerous species with various adaptations for dispersal (cf. Levin & Kerster, 1974; Levin, 1979). For the most part, seeds remain in the vicinity of the seed source. The long-distance component of seed dispersal distributions is poorly understood and difficult to document. It is likely that our impressions of seed dispersal are too conservative owing to our ignorance of the dispersal curve tail (Grant, 1980).

Seed dispersal typically is measured in terms of absolute distance. However, a mean dispersal distance of 25 m in a population of mesophytic climax tree species does not have the same implications as it does for a small prairie herb. For the tree, 25 m would be only 2 or 3 plant diameters (canopies) away, whereas for the herb 25 m would be hundreds of plants from the source. Accordingly, parents and offspring would be near-neighbors in the case of the tree, but widely spaced in the case of the herb. It also follows that half-sibs borne on a single plants will be near-neighbors in the case of the tree, but well dispersed in the case of the herb. Near-neighbor pollination in the former would then result in inbreeding, whereas in the latter it would not. Also, it follows that the gene pool of the tree species would be little homogenized by 25 m dispersal whereas that of the herb would be well homogenized. We may conclude that in this example seed dispersal or seed-mediated gene flow effectively is much greater in the herb than the tree.

The numbers of juxtaposed plant canopies over which seeds are dispersed is easily estimated. *Phlox pilosa* seeds are scattered by capsule dehiscence an average of 1.2 m with a maximum of 3.6 m (Levin & Kerster, 1968). The diameter of a mature plant in a typical site is about 3 dm. Accordingly, seeds are dispersed an average of 4 plant diameters and a maximum of 10 diameters. Seeds of *Liatris aspera* are dispersed an average 2.5 m with a maximum of 9 m (Levin & Kerster, 1969). The diameter of a robust adult is about 20 dm. Accordingly, seeds are dispersed an average of 12 plant diameters and as far as 45 diameters. In *Eucalyptus regnans*, wind-borne seeds travel a mean distance of about 40 m and as far as 125 m (Gilbert, 1958). With plant diameters of 8 m, seeds are being dispersed an average of 5 plant diameters and as far as 15 diameters. These examples are representative of late successional plants and point to the effectively restricted distribution of seeds therein. Mean seed dispersal distances for weedy plants with a well-developed plumose pappus are not available. However, from Sheldon & Burrows's (1973) calculations of dispersability based upon propagule's terminal velocity and resistance coefficients, we may infer that in strong winds seeds of

such weeds as *Cirsium arvense* and *Sonchus arvensis* are transported an average of 20 plant diameters. Plumed propagules of *Salix repens* and *Populus tremula* also may be carried an average of 15 diameters or more. The so-called weedier plants thus are "placing" their offspring farther away than are the late successional species.

The distribution of seed relative to a source may be altered by distance- and density-responsive seed predators as proposed by Janzen (1970). He argued that "no matter how large the seed crop in a given year, or how far the seed from the parent, density-responsive predators will pursue seeds and seedlings until their density is so low that search is no longer profitable." He also postulated that "if seeds are placed or planted at various distances from a parent tree at low density . . . , their survival to well developed sapling stages should increase with distance from the parent." Janzen's postulates have received support from seed predation patterns in *Sterculia apatula* (Janzen, 1972), *Scheelea rostrata* (Wilson & Janzen, 1972), *Juglans nigra* (Stapanian & Smith, 1978), *Andira inermis* (Janzen et al., 1976), and *Datura discolor* (O'Dowd & Hay, 1980), and seedling mortality patterns in *Casearia nitida* (Howe & Primack, 1975) and *Casearia corymbosa* (Howe, 1977). Density-dependent and proximity-dependent predation introduce a differential between potential seed dispersal and actual seed dispersal, the mean and variance of the latter being greater. Since predation tends to increase distance between parents and offspring, and between half-sibs, the result is an opening of the breeding structure of populations.

Interpopulation Gene Flow

The extent of interpopulation gene exchange in nature is unknown. On the other hand, plant breeders have determined distances sufficient to preclude interpopulation contamination of varieties. In many outcrossing crops, more than 5% of the seeds will be hybrid if the distance between populations is about 10 m; and more than 1% of the seeds will be hybrid if the distance is about 500 m (Kernick, 1961; International Crop Improvement Association, 1963). We might be tempted to assume that gene flow in crops is representative of that in natural populations. However, there are several considerations which suggest that gene flow between natural populations may be higher than that in crops over the same distance. First, there is the matter of population size. Natural populations typically are smaller and more patchy in their structure than crop plots. The level of interpopulation hybridization is a function of population size or varietal mass, so that hybridization between populations will increase as population size declines (Fryxell, 1956; Bateman, 1947; Crane & Mather, 1943; Williams & Evans, 1935). Another consideration is the spatial relationships of populations. Plant breeders employ a donor population and one to several recipient populations. All pollen can be traced to that donor population. In nature, a population may receive pollen from several neighboring populations. Even if the levels were low from each source, they are additive, and the sum might have a considerable impact on the genetic structure of the recipient population. Finally, there is the matter of the pollinator. Most animal-pollinated crop plants are serviced primarily by honeybees, whose foraging area is considerably less than other bees and lepidopter-

ans (Heinrich, 1975; Free, 1970). Accordingly, hybridization is lower than might be the case were the same plants subjected to natural pollinators.

The extent to which gene flow fosters the convergence of populations or restricts their divergence depends not only on the frequency of hybridization but also upon the adaptedness of hybrids. The more fit the hybrids the greater the importance of each hybridization event. Are interpopulation hybrids inferior or superior to indigenous plants? In predominantly outbreeding crop species, the vigor and fecundity of hybrids typically increase as the genetic distance between parental strains increases until some critical level of divergence is reached when interactions at a few loci counterbalance the effect of heterozygosity. In maize, heterosis is a positive function of the level of divergence of strains except for the most divergent ones (Moll et al., 1965). In *Nicotiana* (Matzinger & Wernsman, 1967) and *Gossypium* (Mariani & Avieli, 1973), heterosis increases with divergence to the level of related species.

In natural population systems, maximum heterosis also is associated with moderate levels of divergence. Heterosis has been documented in interracial crosses of Norway spruce (Nilsson, 1974), Douglas fir (Orr-Ewing, 1969), and loblolly pine (Woessner, 1972; Owino & Zobel, 1977). Greater heterosis and higher fertility were obtained in the progeny of crosses between *Liriodendron tulipifera* of different populations (often only a few miles apart) than in crosses within the same population (Carpenter & Guard, 1950). Heterosis in *Mimulus* is best developed in hybrids between populations which have undergone moderate degrees of divergence regardless of their geographical relationships (Vickery, 1978). Beltran & James (1974) demonstated heterosis in hybrids between chromosomally homozygous populations of *Isotoma petraea*, the more inbred the populations the greater the vigor of their hybrids. No correlation was found between heterosis and the level of population divergence. The *Isotoma* study is of particular interest because it shows that the genetic structure of populations, as shaped by population size and breeding structure, affects the relative quality of distant pollen parents.

Our knowledge of interpopulation hybrids is based principally upon crosses between populations tens to hundreds of miles apart, and upon performance trials in greenhouses, gardens, or plantations. Of principal concern here are hybrids between neighboring populations or those within pollination range, and how those hybrids would fare in natural populations. Neighboring populations may be well differentiated as a result of selective differentials or random drift. If populations are different by virtue of differential selection and hybrids are intermediate to their parents, then interpopulation hybrids may be ill-fit in either population; it is unlikely they will be better adapted than local residents. On the other hand, if populations have small effective sizes, have diverged as a result of stochastic processes, and are genetically depauperate, then interpopulation hybrids may be superior (heterotic) to local residents in both the egg and pollen parent populations.

Genetic Differentiation

In practice we estimate gene flow in plants from the distributions of pollen and seeds, or from the movements of pollen and seed dispersers. We use dispersal

in one form or another to estimate gene flow. Whereas dispersal of pollen and seeds has some general predictive value with regard to gene flow, dispersal per se does not guarantee gene flow. This point recently was elaborated upon by Endler (1977, 1979) with respect to animals. He concludes that dispersal overestimates gene flow because of the complexities of animal behavior and their life history attributes. In the case of plants I have reached the opposite conclusion. Estimates of gene flow based upon dispersal of pollinators, pollen grains, and seeds tend to underestimate actual gene flow distances because they do not take into consideration pollen carry-over and flight directionality, proximity-dependent cross-compatibility and seed-set, and proximity- and density-dependent seed predation and seedling survivorship, seed pools, genotype-dependent survivorship, and the fitness of interpopulation hybrids. The implications of wider gene dispersal are best understood within the framework of breeding structure and selection models which provide numerical and spatial scales upon which patterns of gene flow may be interpreted.

The breeding structure of populations may be considered in terms of Wright's (1940, 1943, 1946, 1951) neighborhood model. The neighborhood is the area from which any two parents could have come with equal probability. The effective size of a neighborhood is equivalent to the number of reproducing individuals in a circle whose radius is equivalent to twice the standard deviation of the gene dispersal distance (Wright, 1946). Strictly speaking this circle includes 87% of the parents of individuals at its center. The neighborhood size in a plant with pollen and seed dispersal may be described as $N_e = 6.3dr(\Sigma p_i^2/2N_p + \Sigma s_i^2/N_s)$ where p refers to pollen dispersal distance, N_p number of pollen dispersal observations, s the seed dispersal distance, N_s the number of seed dispersal observations, and r the proportion of outcross progeny (Levin & Kerster, 1969). The area of a neighborhood is N_e/d, where d is the genetically effective density. Genetically effective density is approximately the density of flowering plants. The neighborhood describes the scale of gene flow and thus sets the lower limit on the area that can respond to spatially defined disruptive selection (Slatkin, 1973; May et al., 1975; Endler, 1977).

Estimates of neighborhood size and area for several representative herbs and trees are enumerated in Tables 2 and 3. Neighborhood sizes vary from 5 in the facultatively cleistogamic *Lithospermum caroliniense* to 547 in *Viola pedata*. Neighborhood areas also vary widely among species, ranging from less than 20 m^2 in *Viola blanda* and *Phlox pilosa* to over 30,000 m^2 in *Pinus elliottii*. There is also considerable variation within species. The neighborhood sizes of herbs and trees fall within the same range, but the neighborhood areas of trees are considerably larger. The size of the neighborhood determines the level of inbreeding and penchant for genetic drift between sectors of population. For most species in Table 2, the size of the neighborhood is sufficient (>50) to preclude substantial differentiation via genetic drift within a continuous population (Wright, 1943). These values are calculated from dispersal data alone and thus are apt to be underestimates of actual neighborhood sizes.

The area of neighborhoods in plants, especially herbs, is sufficiently small to permit marked differentiation in response to selection over short to moderate distances. If mean gene flow distances were greater than that of dispersal, the

TABLE 2. Neighborhood size and gene flow-selection balance in herbs.

Species	N_e	l[a]	l_c[b]	Cline width[c] Δ = 0.1 m	Cline width[c] Δ = 1000 m	Coefficient of Selection[d]	Reference
Phlox pilosa	75–282	1.6 m	5.1 m	12.5 m	71.1 m	0.03	Levin & Kerster, 1968
Liatris aspera	30–191	1.5 m	4.7 m	11.5 m	67.4 m	0.02	Levin & Kerster, 1969
Liatris cylindracea	165	2.3 m	7.3 m	17.9 m	90.8 m	0.05	Schaal & Levin, 1978
Viola pedata	205–547	2.5 m	7.9 m	19.4 m	95.2 m	0.06	Beattie & Culver, 1979
Viola pensylvanica	310	3.6 m	8.2 m	20.1 m	97.6 m	0.07	Beattie & Culver, 1979
Lithospermum caroliniense	5	1.4 m	4.5 m	11.0 m	65.4 m	0.03	Kerster & Levin, 1968

[a] l = square root of mean squared dispersal distance.
[b] l_c = characteristic length scale of variation of gene frequencies; s = 0.10.
[c] s = 0.10; Δ refers to width of environment transition.
[d] For gene substitution over 30 m.

neighborhood area would increase. Then there would be less isolation by distance within and between populations, and less potential for selective differentiation over short distances, than would be possible with the areas enumerated in Tables 2 and 3.

The relationship between gene flow and selection in shaping local variation patterns in a heterogeneous environment and the spatial scale of such variation is best considered in terms of a one-dimensional gene flow scale l, the square root of the mean squared dispersal distance, rather than neighborhood area (Fisher, 1950; Slatkin, 1973; Endler, 1977). The gene flow distance, l, is related to the neighborhood radius by $r = l\sqrt{2}$. The smaller that l is the greater the isolation by distance between two subpopulations, and the more rapidly and fully these aggregates may respond to local selective differentials. Knowing l, we may calculate the minimum distance over which a population may respond to selection, assuming an abrupt selective change between adjacent environments as in Endler's (1977) ecotone model. This is referred to as the characteristic scale length

TABLE 3. Neighborhood size and gene flow-selection balance in trees.

Species	N_e	l[a]	l_c[b]	Cline width[c] Δ = 0.1 m	Cline width[c] Δ = 1000 m	Coefficient of Selection[d]	Reference
Pinus cembroides	11	17.0 m	53.8 m	131.8 m	342.0 m	0.02	J. Wright, 1953
Pinus elliottii	365	67.8 m	214.4 m	525.3 m	959.7 m	0.25	Wang et al., 1960
Cedrus atlantica	207	74.3 m	234.9 m	575.5 m	911.4 m	0.31	J. Wright, 1953
Pseudotsuga taxifolia	26	18.8 m	59.4 m	145.5 m	365.4 m	0.02	J. Wright, 1953

[a] l = square root of mean squared dispersal distance.
[b] l_c = characteristic length scale of variation of gene frequencies; s = 0.10.
[c] s = 0.10; Δ refers to width of environment transition.
[d] For gene substitution over 300 m.

of variation of gene frequencies (l_c) and is defined as $l_c = l/s$, where s is the maximum difference in fitness between homozygotes in two environments (Slatkin, 1973). Regardless of the spatial heterogeneity in selection pressures, gene frequencies would not vary significantly over a distance less than this length. If the environment changes on a scale less than this length, gene frequencies will respond to selection intensities averaged over the characteristic length. When the scale of variation in the environment is greater than this length, populations can respond to a heterogeneous environment and differentiate into distinctive units with clines between them (May et al., 1975; Endler, 1977).

The characteristic scale lengths, assuming $s = 0.10$, for the plants under consideration vary from 4.7 m for *Liatris aspera* to 234 m for *Cedrus atlantica* (Tables 2 and 3). If the selective differential between the environments is less, the distances would be greater and vice versa. As we might expect, populations of herbs are better able to respond to local environmental heterogeneity than trees. Were the intensity of selection reduced by an order of magnitude, the characteristic scale length would increase roughly 3 times. If the mean gene flow distance were twice the dispersal distance (l in Tables 2 and 3), then the characteristic scale lengths shown in Tables 2 and 3 would have to be doubled.

Consider next the width of clines between two habitat types which are juxtaposed, so that the transition occurs over a very short distance, less than the characteristic scale length. Suppose that genotypes AA, Aa, and aa have fitness of $1 + s$, 1 and $1 - s$, respectively, in one habitat, and $1 - s$, 1, and $1 + s$, respectively, in the other. The width of a cline from p = 1 to p = 0 is 2.45 l_c (May et al., 1975). Using 0.10 as the value of s (as above), we find that the width of clines varies from 11 to 20 m for herbs (Table 2) and from 132 to 575 m for trees (Table 3). It is evident that marked differentiation, in this case gene substitution, can occur over relatively short distances in response to moderate selective differentials. This is the consequence of restricted gene flow. If the actual gene flow distances were twice those described (l in Tables 2 and 3), then the width of the cline would double.

The transition between environments may be gradual instead of abrupt. Suppose that one homozygote is best fit for one environment and the other homozygote the other, that the fitnesses of homozygotes varied over a 1000 m gradient, and that the fitness relationships are as given in the previous example. The width of the cline is $2.40(l_c^2\Delta)^{1/3}$ where Δ is the transition distance over which both homozygote fitnesses are changing relative to one another (May et al., 1975). The width for the herbs is between 71 and 98 m (Table 2), and for the trees is between 342 and 960 m (Table 3). This illustration shows that substantial differentiation may occur over moderate distances along environmental gradients. Were the actual gene flow distances twice those inferred from dispersal distances, the clines would be twice as wide.

Finally let us ask the intensity of selection that would be necessary to bring about gene substitution (p = 1.0 to p = 0) over a span of 30 m for herbs and 300 m for trees. The value of s may be estimated from the following relationship: maximum slope of gene frequencies $\sim\sqrt{s/3l}$, where the slope is the difference in gene frequencies/distance and l is the root mean square of the migration distance as above (Slatkin & Maruyama, 1975). The selection coefficients necessary to

bring about gene substitution over 30 m in herbs are surprisingly small, less than .07 (Table 2). If the actual gene flow distances were greater than dispersal distances, the intensity of selection necessary for gene substitution would be greater. The selection coefficient necessary to bring about gene substitution over 300 m in trees is weak in some species and strong in others (Table 3). If the actual gene flow distances were greater than dispersal suggests, substitution would not be possible in *Cedrus atlantica* and *Pinus elliottii*.

The spread of an advantageous gene across populations also is dependent upon gene flow. It is intuitively obvious that the greater the distances over which genes move per generation the more rapid the spread of the advantageous gene. Fisher (1937) found that the advance of advantageous genes or velocity of the wave of gene increase along a linear habitat can be described as $v = \sigma(2m)$, where σ is the standard deviation for gene flow distance and m is the selective advantage. The standard deviation for the plant species considered earlier may be obtained from Tables 2 and 3, recognizing that the gene flow distance $l = 2\sigma$. The spread of an advantageous gene in *Phlox pilosa,* assuming that the selective advantage is $s = 0.10$, is 0.16 m per generation. In *Cedrus atlantica,* the rate is 7.4 m per generation. Even if the selective advantage is large the spread is slow. If $s = 0.5$, the rate of spread is still only 0.8 m per generation in *Phlox* and 37 m in *Cedrus*. The progress of the advantageous gene would be at least four times greater in a two-dimensional population with the same gene flow characteristics (Wright, 1969).

In the case of a linear array of discontinuous populations, the advantageous genes would progress in a wavelike fashion, with the velocity being a function of interpopulation gene flow and time to fixation within populations (Slatkin, 1976). The velocity of the wave of an advantageous gene may be estimated from the tabulations of Slatkin (1976). Consider a rather realistic set of circumstances in which populations are 1 km apart, where the population size (N) equals 500, adjacent populations exchange 1 individual per generation (m = 1), and the advantage of a gene is 10%. Under these circumstances, the rate of spread is about 20 m per generation. If gene flow were reduced by an order of magnitude (m = 0.1), the velocity would be about 11 m per generation.

Although gene exchange is most likely to occur between adjacent populations, there may be some between distant populations. These long-distance events would substantially increase the rate of spread of an advantageous gene. Returning to a linear array of populations and the tabulations of Slatkin (1976), and assuming that on the average 0.01 individual moves between populations 10 steps apart with populations of 500 and a selective advantage of 10%, the rate of spread would be about 30 m per generation. This compares with 20 m per generation with gene flow between adjacent populations.

Models of gene migration in a one-dimensional array pertain to population systems distributed along rivers, shorelines, and other such linear habitats. Most plant population systems are distributed in two dimensions. The rate of spread of an advantageous gene in a two-dimensional array has not been described. However, it will be greater than in a one-dimensional array because there are more pathways over which a gene could move between populations (Slatkin, 1976). The rate of spread is determined primarily by the lag time associated with

the movement of genes between populations, i.e., the time between gene entry and its attainment of a frequency such that it might be transported by a migrant (seed or pollen). Let us assume that in a two-dimensional array the level of gene exchange between populations increases by a factor of two, so that there are 2 migrants per generation between populations of 500 ($s = 0.10$). The rate of spread of an advantageous gene will be 23 m per generation compared to 20 m when there was only 1 migrant per generation. If the number of migrants is doubled in the aforementioned model of gene exchange between populations 10 steps removed (from 0.01 to 0.02 individual per generation), the rate of spread increases from 30 m per generation to 52 m. If the number of migrants increases by a factor of 5 due to 2-dimensional gene exchange, the rate of spread increases to 86 m per generation. The progress of an advantageous gene through a population system remains moderate even with very liberal gene-flow estimates.

Depending upon whether a plant was predominantly selfing or outcrossing and on the means of seed dispersal, the wave of advance of a beneficial gene at high frequency probably would range from less than 5 m to more than 50 m per generation. At these rates a beneficial gene would not have time to dominate much beyond the region in which it originated. Using 25 m per generation for illustrative purposes, it would take 4000 years for a high frequency wave to move 100 km in an annual plant. Even if the rate were 100 m per generation, it would take 1000 years for a wave to cover this distance or over an area about 10,000 km^2. This constitutes only a small portion of the range of most species. The rate of spread will be even slower in perennials, because the rate is measured in terms of distance per generation. The rate of spread in a short-lived perennial herb (generation time of 10 years) would be one-tenth that described, so that the range of distances per year would range from less than 0.5 to around 5 m. For a long-lived perennial, the rate would be reduced by an additional 50% or more. Clearly, with the biological processes we are envisioning, novel adaptive mutations originating in one population cannot rise to prevalence throughout a significant portion of a species range.

In summary, I have argued that estimates of gene flow within and among populations which are based upon the movement of pollinators, pollen, and seeds tend to be too small. On the other hand, the scale of dispersal is so small that even if gene flow distances were twice those of dispersal, differentiation within populations under moderate disruptive selection pressure, and interpopulation divergence with very weak selective differentials would still be possible. Indeed populations more than a few kilometers apart may be completely isolated by distance and thus free to diverge along avenues independent of those taken by other populations. Gene flow appears so restricted that novel adaptive mutations would be confined to relatively small portions of species ranges.

The view of Ehrlich & Raven (1969) that gene flow is not a prime integrating force within species still seems valid. Indeed, if cohesion does occur as a consequence of gene exchange, ostensibly it is within continuous subpopulations, discontinuous subpopulations, or tightly knit clusters of neighboring populations. These narrowly circumscribed ensembles thus are the effective units of evolution.

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EVOLUTION OF SEXUAL SYSTEMS IN FLOWERING PLANTS[1]

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ABSTRACT

The diversity of sexual systems in plants has been generally attributed to selection for an optimal amount of genetic recombination. However, sexual systems such as hermaphroditism (including heterostyly), monoecism, andromonoecism, gynomonoecism, dioecism, androdioecism, and gynodioecism may also be viewed as different patterns of relative resource allocation to paternal and maternal functions to optimize paternal and maternal reproductive success in different ways. These different patterns may arise in large part in response to reproductive competition resulting from sexual selection. But the efficacy of sexual selection in zoophilous species is mainly determined by pollinator behavior. It follows then that the evolution of a particular sexual system must be influenced by the dynamics of the pollination system. The role of pollinators in the evolution of sexual systems is examined by considering several types of interactions between flowers and pollinators. The role of cost-sharing between paternal and maternal functions in pollinator attraction is stressed in the evolution of hermaphroditism. Andromonoecism is considered in terms of loss of pistils in that part of the flower crop which is produced merely to attract pollinators and/or to fulfill male function. In the evolution of andromonoecism to monoecism, the role of stamens of hermaphroditic flowers in the functional integrity of the pollination system is evaluated. The importance of long mouth parts of pollinators to promote compatible pollinations in the evolution of heterostyly is pointed out. The evolution of protogyny is considered in relation to long inhabitation of pollinators in flowers and inflorescences. The evolution of dioecism is examined in relation to the ability of pollinators to respond to minor changes in floral resources thereby altering the patterns of pollen donation and pollen receipt. Finally, the importance of stamens in hermaphroditic plants in attracting pollen collecting bees is emphasized in the maintenance of androdioecism. The development of a general hypothesis to explain the diversity of sexual systems will require not only a comprehensive knowledge of pollination ecology but also a revision of the sexual system classification that will take into account functional gender rather than intrinsic gender estimates based solely on morphology.

The flowering plants display a wide variety of sexual systems ranging from obligate selfing in association with self-compatibility to obligate outcrossing in conjunction with self-incompatibility (Darlington, 1958; Grant, 1958; Lewis & John, 1963; Mather, 1973; Solbrig, 1976; Jain, 1976; de Nettancourt, 1977). In addition, genetic recombination may be partially or completely circumvented by facultative or obligate apomixis (Stebbins, 1950). Superimposed upon these genetic systems are such temporal and morphological mechanisms as protandry, protogyny, heterostyly, monoecism, andromonoecism, gynomonoecism, dioecism, gynodioecism, and androdioecism, that are also presumed to regulate the level of outcrossing (see Darwin, 1877; Müller, 1883; Mather, 1940; Lewis, 1942; Baker, 1959; Jain, 1961; Lloyd, 1975a; Ross, 1970; Charlesworth & Charlesworth, 1978; Charlesworth & Charlesworth, 1979; Ganders, 1979).

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Darwin (1877) was the first to comprehensively document and explain the diversity of sexual systems in plants. His work, including his studies of the effects of self- and cross-fertilization on the fitness of plants (Darwin, 1876), had a major impact on current ideas about the evolution of sexual systems. After the development of the synthetic theory of evolution, the genetic implications of the diversity in sexual systems emerged as a major issue in the evolutionary biology of plants, and selective pressure for an optimal amount of recombination came to be viewed as *the essential force* in the evolution of sexual systems (Stebbins, 1958; Darlington, 1958; Grant, 1958; Baker, 1959; Lewis & John, 1963; Mather, 1973). In turn, patterns of plant sexuality came to be regarded as outcrossing mechanisms and regulators of genetic recombination.

Recently, models have been proposed for the evolution of some sexual systems that do not invoke outcrossing as the main selective force. Charnov et al. (1979) and Maynard Smith (1978) have postulated the evolution of hermaphroditism, dioecism, and gynodioecism in terms of optimal allocation of resources to male and female reproduction. Janzen (1977) has commented upon the effect of optimal mate selection on the evolution of monoecism and dioecism. The evolution of dioecism has also been examined in the context of sexual selection (Willson, 1979; Charnov, 1979; Bawa, 1980a; Givnish, 1980), dispersal by avian frugivores (Bawa, 1980a; Givnish, 1980; see also Lloyd, 1981), foraging behavior of pollinators (Beach & Bawa, 1980; Beach, 1981), and disruptive selection resulting from differential utilization of habitats by male and female plants (Freeman et al., 1980). Pleiotropic effects of male sterility gene have been implicated in the evolution of gynodioecism in *Plantago lanceolata* (Krohne et al., 1980).

There are two major difficulties with the general explanation that selective pressure for outcrossing or an optimal amount of recombination underlies the diversity of sexual systems. First, the argument might explain the evolution of self- versus cross-fertilization but does not account for the tremendous diversity of sexual systems, almost all of which facilitate outcrossing (Willson, 1979). It is possible that different sexual systems result in different levels of outcrossing, but there is no evidence that as one moves from andromonoecism and gynomonoecism to dioecism, one moves along a consistent gradient of increasing cross-pollination. In fact, several andromonoecious, monoecious, and gynodioecious species are known to be self-incompatible (see below). Second, it has been demonstrated that the ability to self- or cross-fertilize, by itself, is often not a good indicator of the level of recombination in natural populations (see Allard, 1965; Jain, 1976), because the level of recombination is determined not only by the sexual system but also by the mechanics of crossing-over, linkage (Darlington, 1958; Lewis & John, 1963), the foraging behavior of pollinators and seed dispersal agents (Levin & Kerster, 1974), and selection against inbreeding (Jain, 1976).

Our discussion of the evolution of flowering plant sexual systems is developed with repeated emphasis of some basic ecological differences between paternal and maternal reproductive success (Horovitz & Harding, 1972; Charnov, 1979; Lloyd, 1979a, 1980b; Willson, 1979). Our approach is based on two proposals. The first is that paternal reproductive success is limited by a plant's ability to disperse pollen to conspecific stigmas, whereas maternal success is usually limited by the amount of nutritional resources available for developing embryos, seeds,

and fruits (Bateman, 1948; Charnov, 1979; Lloyd, 1979a). Thus, paternal and maternal reproductive success may be optimized in different ways. The second proposal is that conspecific pollen movement, in particular patterns of dispersal and receipt, is greatly constrained by the type of pollinator or pollination system. We suggest that: (a) sexual systems such as hermaphroditism (including heterostyly), monoecism, andromonoecism, gynomonoecism, dioecism, androdioecism, and gynodioecism be viewed as different patterns of relative resource allocation to paternal and maternal functions to optimize paternal and maternal reproductive success in dissimilar ways (see also Charnov et al., 1976; Lloyd, 1979a); (b) that these different patterns arise mainly in response to reproductive competition resulting from sexual selection (Willson, 1979); and (c) that the evolution of a particular pattern is constrained largely by the dynamics of the pollination system. The last point, being new and a crucial element in our proposal, needs elaboration.

Although sexual selection influences the relative *allocation* of resources to male and female functions (Charnov, 1979; Willson, 1979), the actual *distribution* of these resources in the form of male, female, and bisexual flowers is largely determined by the ecology of the pollination system. In the case of biotic pollination, this is a result of the foraging behavior of pollinators determining the pattern of pollen removal and pollen receipt, and consequently the effective role of flowers as pollen donors and pollen receivers (Willson & Price, 1977; Pyke, 1978). But the foraging behavior of pollinators itself is influenced by selection in plants for variation in floral rewards in space and time to optimize the movement of pollinators and thereby pollen flow. Variation in floral rewards may be achieved through changes in the relative proportions of male, female, and bisexual flowers, or of pollen donors and pollen receivers, because male flowers may only produce pollen or pollen as well as nectar, whereas female flowers generally secrete only nectar except in cases involving mimicry (Baker, 1976; Bawa, 1980b). Many sexual systems may simply represent such variations that have coevolved with the foraging behavior of pollinators. Our treatment of sexual systems here emphasizes such coevolution and the role of pollinators in differentially influencing paternal and maternal reproductive success.

In addition to the putative ecological and energetic advantages of different patterns of floral sexuality that we review below, a number of attempts have been made to elucidate the adaptiveness of hermaphroditic organisms (in the broad sense, to include, for example, monoecious plants) over unisexual individuals (Baker, 1967; Maynard Smith, 1978; Heath, 1977; Charnov, 1979; and see Lloyd, 1981, for several additional references). Although these proposals are relevant to the adaptive nature of hermaphroditism vs. unisexuality at the individual level, we limit our discussion here to the ecology of floral sexuality.

We have avoided the use of the term *breeding system* throughout the paper in favor of *sexual system*. This seems more appropriate as it does not carry the implication that plant gender is the sole result of selection for a certain level of genetic variability. The sexual system does include those factors that directly influence the level of outcrossing, but we view the distribution of male and female functions in space and in time, and the ecological interactions among individuals that mate with each other, as being primarily the result of the coevolution between sexual partners and also between flowers and pollinators.

TABLE 1. Standard classification of flowering plant sexual systems as currently used.[a,b]

A. Systems based on the spatial distribution of male and female reproductive organs.
- I. Sexually monomorphic[c] systems characterized by only one gender class of individuals.
  1. *Hermaphroditism:* Plants bear only bisexual flowers.
  2. *Monoecism:* Plants bear male and female flowers.
  3. *Andromonoecism:* Plants bear bisexual and male flowers.
  4. *Gynomonoecism:* Plants bear bisexual and female flowers.
- II. Sexually dimorphic species characterized by two gender classes of individuals.[d]
  1. *Dioecism:* Plants bear either male or female flowers.
  2. *Gynodioecism:* Plants bear either female or bisexual flowers.
  3. *Androdioecism:* Plants bear either male or bisexual flowers.

B. Systems based on the temporal distribution of male and female organs.
1. *Protandry:* Pollen removed from the anthers before stigmas attain receptivity.
2. *Protogyny:* Stigmas become receptive before anthers release pollen.

C. Systems based on the presence or absence of self-incompatibility alleles.
1. *Self-incompatibility:* Plants polymorphic with respect to the presence of self-incompatibility alleles; pollinations involving pollen and stigma sharing the same self-incompatibility alleles, including self pollinations, result in no fruit set.
2. *Self-compatibility:* Plants monomorphic and without the presence of self-incompatibility alleles; all pollinations, including self-pollinations, result in fruit set.

D. Systems based on variation in style and stamen length.
1. *Distyly:* Two types of individuals that bear different forms of flowers, pin flowers with long styles and short stamens and thrum flowers with short styles and long stamens. Self-pollination and pollination within the morphs generally incompatible.
2. *Tristyly:* Three types of individuals that bear long-, mid-, or short-style flowers. Anthers occupy two out of the possible three positions, for example, long-style flowers have anthers at the short and mid position, mid-style flowers have anthers at the short and long position, and so on. Compatible pollinations result from crosses involving stigmas and anthers at the same level.

[a] In addition to the systems described below, there exist other systems such as cleistogamy and various forms of apomixis (see Stebbins, 1950).

[b] The systems described below are not mutually exclusive.

[c] The use of monomorphic and dimorphic follows that of Lloyd (1972a, 1979a, 1980a). These terms should not be confused with their application elsewhere, usually to describe floral heteromorphism based on variation in style and stamen length (Ganders, 1979).

[d] Plants of sexually dimorphic species may exhibit considerable variation in sex expression, especially in gynodioecious species in which individuals with bisexual flowers may be partially or fully female-sterile.

Classification of Sexual Systems

Lloyd (1980a) has pointed out difficulties with the existing classification of flowering plant sexual systems. The descriptive terms used by taxonomists and ecologists alike, being derived from Linnaeus's (1737) artificial classification of flowering plants based on sexual systems, are typological, qualitative, and defined by arbitrary limits. Because of this and for additional reasons (see Discussion) the available terminology neither adequately describes patterns of sexuality in plants, nor their effective gender. The work of Lloyd (1980a) in establishing quantitative measures of plant gender is of great value. However, for purposes of our initial discussion, we will use the traditional sexual system categories as shown in Table 1.

Sexually Monomorphic Systems

Hermaphroditism.—We use the term *hermaphrodite* in a restricted sense to designate those species with simultaneously bisexual flowers.

Most flowering plants have only bisexual flowers (Yampolsky & Yampolsky, 1922; Lloyd, 1981) and have their pollen distributed by a diverse array of biotic

and abiotic agents (Faegri & van der Pijl, 1971). The ecological and evolutionary significance of bisexuality was emphasized by Baker & Hurd (1968), who suggested that the coevolution of hermaphroditic flowers with animal pollination might be an important advancement by early angiosperms since pollen-producing and pollen-receiving organs in the same flower allowed for efficient simultaneous deposition and removal of pollen. Baker & Hurd (1968) and Crepet (1979) have argued that since the original attraction of visiting insects for flowers was the presence of pollen for food, there would have been no incentive for pollinators to visit a female flower, giving an advantage to plants with hermaphroditic flowers.

Charnov et al. (1976) and Maynard Smith (1978) have proposed that bisexual flowers sometimes represent the optimal use of energetic resources available for reproduction, since the fixed costs associated with male and female functions would be shared. Such costs would include, for example, bracts subtending flowers, pedicels supporting flowers, flower parts that serve in pollinator attraction, and nectar rewards.

It is significant that in contrast to sexually dimorphic species, hermaphroditic species generally have large, showy flowers (Bawa & Opler, 1975; Bawa, 1980a). Dioecism is poorly represented in the Araceae and Palmae in which the energetic investment into large bracts (spathes) and inflorescence stalks (spadices) presumably far exceeds the investment into very small male and female flowers. These correlations are consistent with the hypothesis that whenever common costs of male and female functions are large relative to the costs of the production of the two types of gametes, hermaphroditism may be favored over unisexuality (Heath, 1977; see also Lloyd, 1979a). Note, however, that Heath (1977) proposed the hypothesis to explain the evolution of hermaphroditism vs. unisexuality in animals and that he defined hermaphroditism in a broad sense to cover monoecious as well as hermaphroditic species.

It is difficult to assign a single most important selective force to the evolutionary rise and maintenance of bisexual flowers because, ecologically, hermaphroditism encompasses a diverse group of plants. The production of functional male and female gametes does not mean that either the flower or the individual plant contributes to the next generation equally via the male and female pathways (Horovitz & Harding, 1972; Lloyd, 1979a; Willson, 1979). Willson & Rathcke (1974) and Willson & Price (1977) have provided evidence that in milkweeds (*Asclepias* spp.) an increase in the number of flowers in an inflorescence results in a greater genetic contribution via pollen to the next generation, but not via ovules. In addition, phenomena such as dichogamy, self-incompatibility, and heterostyly make hermaphroditic species a complex assemblage of plants.

Andromonoecism.—Andromonoecism has been reported in species pollinated by bats (Heithaus et al., 1974), bees (Bell & Lindsey, 1978; Symon, 1979; Bertin, 1981), bees and flies (Primack & Lloyd, 1980), hummingbirds (Bertin, 1981), and moths (Bawa, unpublished data). In grasses, andromonoecious species are wind pollinated (Connor, 1979).

The evolution of andromonoecism has been generally ascribed to selective pressure for increasing cross-fertilization (e.g., Heithaus et al., 1974), but this explanation is incomplete for several reasons (Primack & Lloyd, 1980), including the existence of self-incompatibility in several andromonoecious species (Zapata

& Arroyo, 1978; Bawa, unpublished data), and thus other selective forces for the evolution of the sexual system should be considered.

It is a common observation that many hermaphroditic plants generally bear many more flowers than the number of fruits that are matured (see Bawa, 1974, for fruit/flower ratios in several species). Those flowers that do not set seed may function to either attract pollinators and/or to disperse pollen (Willson & Price, 1977; Lloyd, 1979a). Andromonoecism can simply be regarded as representing the situation in which nonfunctional pistils are aborted prior to flowering in those flowers that are destined to serve male or attraction functions (Zapata & Arroyo, 1978). However, it is noteworthy that andromonoecism, though widely distributed, is relatively rare as compared to hermaphroditism, whereas the phenomenon of "excess" flower production is very common in flowering plants. The question then arises as to the significance of pistils in hermaphroditic flowers that largely act as pollen donors. Three possibilities might be considered. First, in many species, especially those with extremely specialized pollination mechanisms, e.g., Apocynaceae and Orchidaceae, the abortion of pistils could disrupt the pollination system by structurally perturbing the floral morphology. Second, the abortion of pistils in many flowers before pollination could restrict the efficacy of selection on progeny acting through control over pollen germination, pollen tube growth, and embryo and fruit abortion. Third, pistils may not be aborted in most species because there is no predictability before pollination with respect to the fate of flowers as pollen donors and pollen recipients (Lloyd, 1980b).

Additional factors in the evolution of andromonoecism have been recently explored by Primack & Lloyd (1980).

Gynomonoecism.—As compared to andromonoecism, gynomonoecism is restricted in its distribution, being known in less than half a dozen families (Yampolsky & Yampolsky, 1922). The Compositae contains the greatest number of gynomonoecious taxa (Loyd, 1979a). Unfortunately, unlike andromonoecism, detailed information about the pollination biology of gynomonoecious species is not available. In the Compositae gynomonoecism results from the sterilization of stamens in the ray (peripheral) florets of the inflorescence. By being petaloid the ray florets enhance the attractiveness of the inflorescence consisting of small flowers. This gives the inflorescence a flowerlike structure, and makes it a functional pollination unit. It is possible that in this family the selective pressure for attractive petaloid ray florets has led to the sterilization of stamens; the large size of male-sterile florets in the Compositae, and of male- and female-sterile flowers in *Viburnum* and other genera raises the possibility that the resources expended in stamens and pistils may be easily reallocated to other floral organs such as petals. Indeed, by attracting pollinators, ray florets in the Compositae influence the level of outcrossing. However, a consideration of gynomonoecism as a pollination rather than an outbreeding system makes it easier to explain why the vast majority of gynomonoecious species occur in the Compositae.

Lloyd (1979a) suggests two other factors to account for the evolution of gynomonoecism in the Compositae. One is that the increase in the number of "polliniferous" flowers in the capitulum would result in neither greater floral display nor an increase in the number of visits by pollinators since it is the capitulum rather than the individual flowers that functions as the unit of attraction. The

other is that in a capitulum composed of uniovulate flowers, gynomonoecism may be the only way to increase the number of seeds without increasing the number of "polliniferous" flowers.

Monoecism.—The sexual specialization of flowers represented by andromonoecism and gynomonoecism is carried a step further in monoecious taxa that are characterized by the presence of male and female flowers on the same plant. Contrary to the popular viewpoint (Yampolsky & Yampolsky, 1922; Grant, 1951; Stebbins, 1951; Faegri & van der Pijl, 1971; Charlesworth & Charlesworth, 1979) monoecism is not confined to wind-pollinated plants. In tropical forests a large number of zoophilous species are monoecious. The vast majority of monoecious species in a dry deciduous and a wet evergreen forest in the lowlands of Costa Rica are insect pollinated, a few are hummingbird pollinated (Bawa, unpublished observations).

It has been argued that monoecism has evolved as a result of the selective advantages of cross-fertilization (e.g., Maynard Smith, 1978), though Godley (1955) has demonstrated the presence of self-incompatibility in several species. We propose that evolution of monoecism represents the continuation of the trend seen in andromonoecious species towards the specialization of flowers into pollen donors and pollen recipients which is due in part to sexual selection and in part to the mechanics of pollination. Monoecism can arise in one step from andromonoecism by the sterilization or abortion of the stamens in hermaphroditic flowers. In relation to the role of pollinators in the evolution of monoecism, we discuss the conditions under which andromonoecism might evolve into monoecism and the conditions under which andromonoecism remains stable.

Selection for the sterilization or abortion of stamens in hermaphroditic flowers may occur under two conditions. The first condition is when pollen in the flowers interferes with the deposition of incoming cross-pollen (Bawa, 1980a). Such interference is likely when the pollination mechanism is imprecise and flowers are small and closely aggregated in an inflorescence, e.g., Araceae, Euphorbiaceae, Moraceae, Palmae, and others. In many taxa of these families, not only is there spatial separation, but also temporal separation of male and female flowers, suggesting perhaps the role of interference as well as sexual selection in the spatial and temporal differentiation of male and female functions. Interference is also likely when pollen is picked up from and deposited on the inflorescence during the same foraging trip, as is the case in some protogynous, monoecious aroids. In other words, if the male and female phases cannot be separated in time in the same flower, they might be separated in space, and by further evolution in space and time. It is noteworthy that many andromonoecious species have large flowers, when contrasted with monoecious species, and, furthermore, these flowers are not very closely aggregated in inflorescences. But in andromonoecious Umbelliferae the flowers are small, clustered together, and even occur in dense capitate heads (Webb, 1980). However, the temporal separation of male and female phases in bisexual flowers, as well as at the level of inflorescences and individuals, is very pronounced (Müller, 1883; Cruden & Hermann-Parker, 1977).

Second, male sterility in hermaphroditic flowers may evolve when the optimal conditions for female reproductive success (pollen receipt) and for male repro-

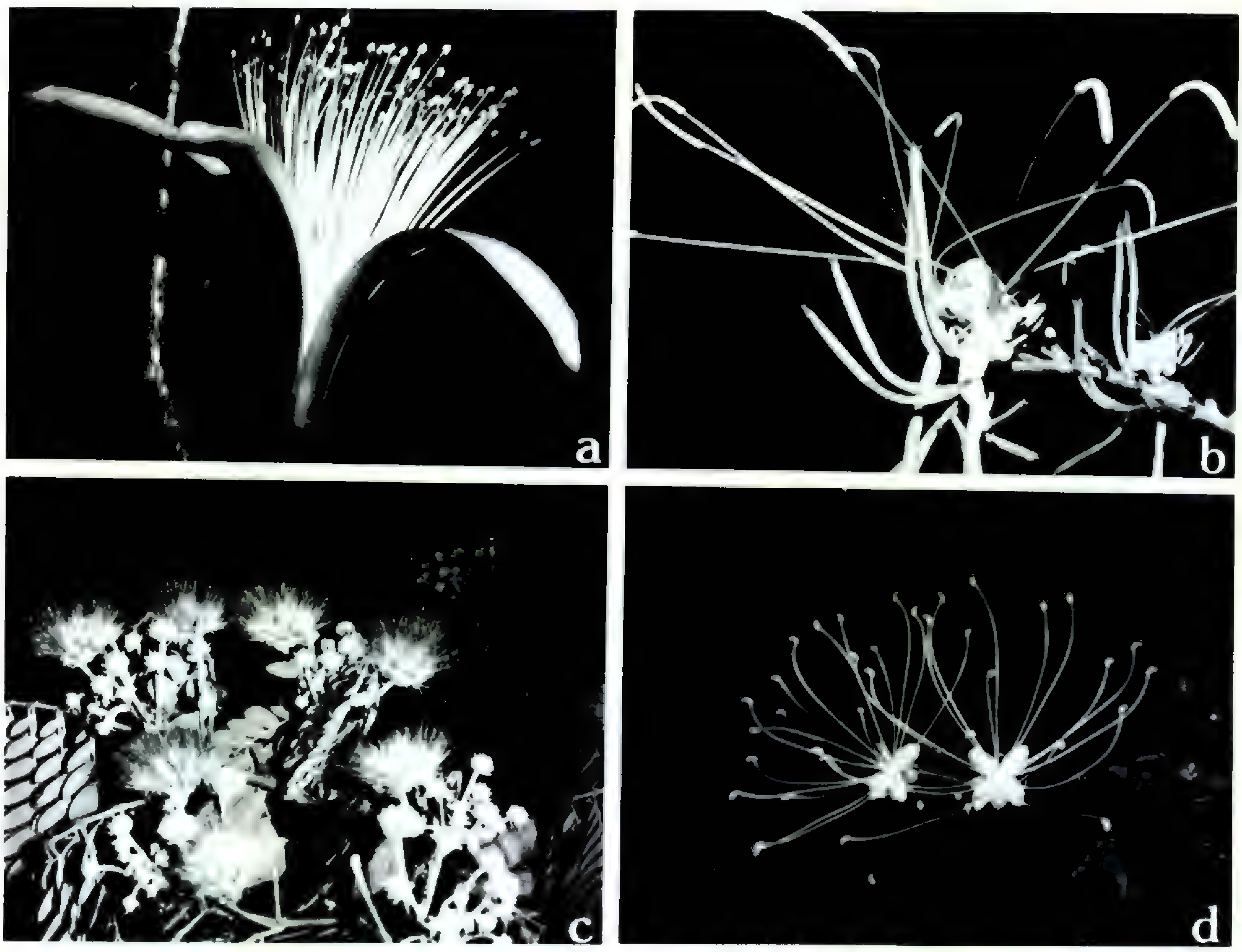

FIGURE 1. Hermaphroditic flowers of *Bombacopsis quinata* (a), *Bauhinia pauletia* (b), *Pithecellobium saman* (c), and *Capparis* sp. (d), to show the importance of stamens in the maintenance of andromonoecism (see text for details). All species, except the particular species of *Pithecellobium* shown here, are andromonoecious; however, andromonoecism has been found by us in some species of *Pithecellobium* closely similar to this particular species. The species are from lowland dry deciduous forest in Costa Rica; Photographs (a) and (b) are by P. A. Opler.

ductive success (pollen donation) are vastly different and strongly influenced by the position of male and female flowers (Heslop-Harrison, 1972). For example, in zoophilous plants where pollinators typically forage from the bottom towards the top in one-day inflorescences, one may expect female flowers at the bottom and male at the top of the inflorescence, as is the case in many monoecious species of the Euphorbiaceae.

Under certain conditions pollinators may select against the loss of sterilization of stamens in the hermaphroditic flowers of andromonoecious species; they thereby impose constraints upon the evolution of andromonoecism towards monoecism. For example, in those cases where the stamens play a large role in the integrity of the pollination system, there would be strong selection against their loss. In andromonoecious species such as *Bauhinia pauletia*, *Bombacopsis quinata*, and *Capparis pitteri* the loss of stamens would destroy the integrity of the flowers or the attractiveness of the inflorescence (Fig. 1). In many mimosoid legumes, the organization of the flowers is largely dependent upon stamens (Fig. 1c) so that one would not expect the andromonoecious species (known to occur in *Albizzia*, *Calliandra*, and *Pithecellobium*, W. Haber, pers. comm.) to evolve

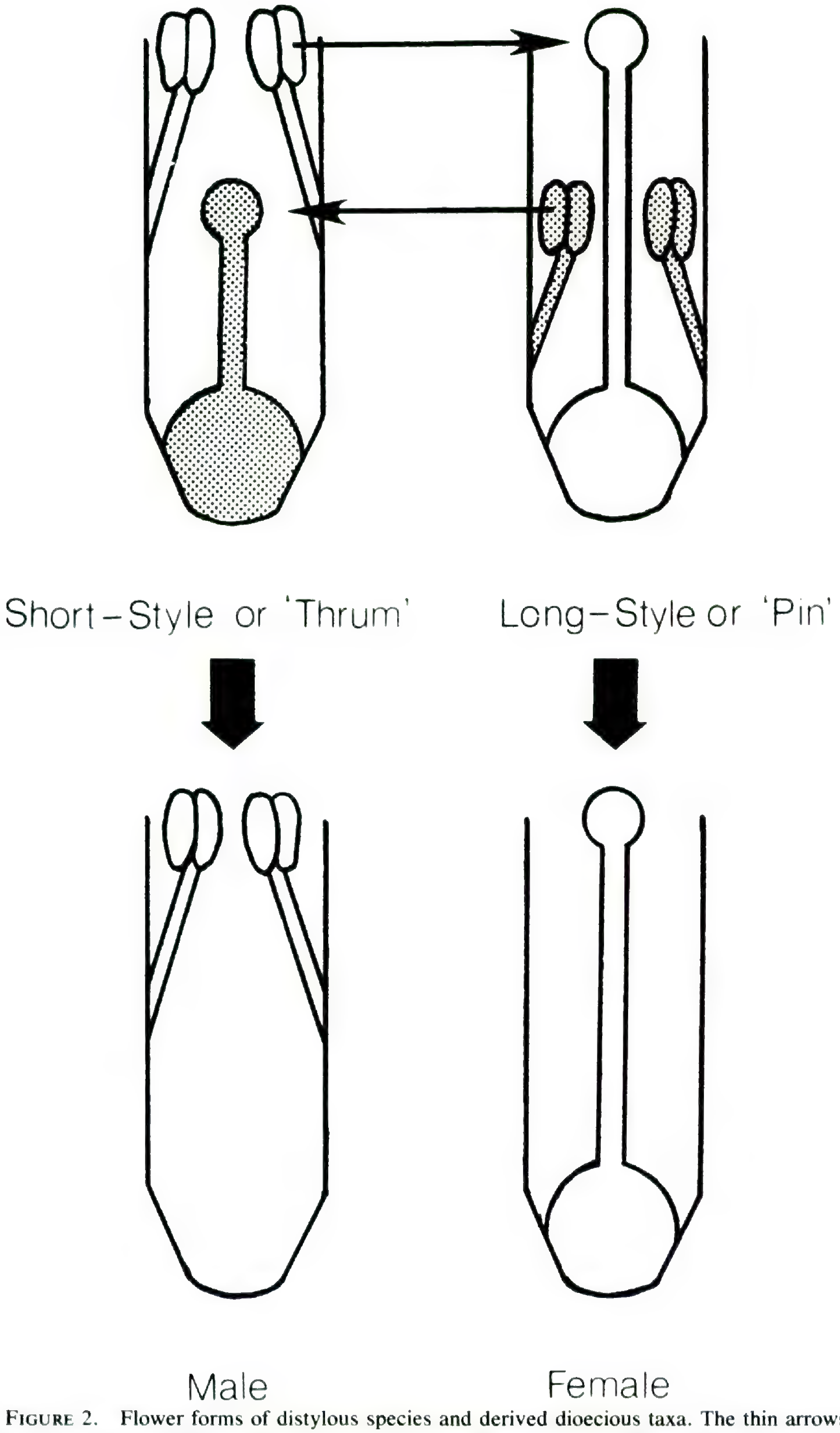

FIGURE 2. Flower forms of distylous species and derived dioecious taxa. The thin arrows between the upper pair of flowers indicate the pollinations that result in fertilization in distylous plants.

into monoecious taxa. In *Solanum*, another genus where andromonoecism is common, stamens may not only play a part in the attraction of the pollinators, but also offer the sole reward to the pollinators since the flowers contain no nectar (Anderson, 1980; W. Haber, pers. comm.). In andromonoecious *Leptospermum* of the Myrtaceae stamens again may be crucial in attracting the flower visitors (Primack & Lloyd, 1980). For *Aesculus pavia*, Bertin (1981) suggested the role of pollen as a food reward in preventing the evolution of andromonoecism to monoecism.

It is not certain if monoecism generally evolves from andromonoecism. There is little discussion of different evolutionary pathways to monoecism in the literature (but see Lloyd, 1972a, 1972b, 1975b). Regardless of the evolutionary pathways involved, selective forces other than those associated with pollination may have also played a role in the evolution of this sexual system.

Heterostyly.—The flower heteromorphisms characteristic of distyly and tristyly have from the earliest study been recognized as structural adaptations to promote disassortative pollination, i.e., the movement of pollen between incompatibility groups (Darwin, 1877). Heterostyly was probably the first sexual system to be recognized as partly an ecological phenomenon.

Distyly, the most common expression of heterostyly is usually associated with gamopetalous, tubular flowers and pollination by relatively long-tongued lepidopterans, hymenopterans, or hummingbirds. The significance of this tripartite relationship among the sexual system, flower morphology, and mode of pollination lies in the fact that the efficacy of pollen transfer from short stamens to short styles (or long stamens to long styles) is contingent upon the deposition of pollen at different locations on the mouth parts of the pollinators. The corolla tube must be relatively long and narrow to allow only restricted access by nectar-seeking probes in order to assure the accurate localization of pollen deposition on the vector, thus promoting subsequent pollen transfer between stamens and styles of the same length.

Most heterostylous species are self-incompatible (Ganders, 1979). The evolution of the self-incompatibility system, which prevents both self-fertilization and mating between plants of the same flower form, probably occurred before the rise of the associated floral hetermorphisms (Ganders, 1979). It is most likely that the morphological features of distyly and tristyly, as part of the pollination system, arose as a response to the appearance of a limited number of incompatibility groups in order to increase disassortative (compatible) pollination and thus a plant's reproductive output (Ganders, 1979; Beach & Kress, 1980). Clearly, both the function and the adaptive basis for the evolution of heterostyly can only be understood by considering the breeding system as an ecological phenomenon: an adaptation to manipulate pollinator movements and pollen flow.

The role of pollinators in the evolution of sexual systems is demonstrated more markedly by the conversion of distyly into dioecism (Fig. 2). This change,

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The heavy vertical arrows represent the evolutionary pathways that have given rise to unisexual flowers. Vestigial styles and stamens are not shown in unisexual flowers. In most cases the change from distyly to dioecy is accompanied by a reduction in the size of the corolla tube. (See Beach & Bawa, 1980, for details)

from one outbreeding system to another has occurred in several genera in the families Boraginaceae and Rubiaceae (Baker, 1958; Lloyd, 1979b; Beach & Bawa, 1980). In every known case where dioecism has evolved in this way, the ancestral long-style form has become female, and the short-style plants have become males (Fig. 2). This would not be the result if selection for unisexuality was unrelated to the ancestral flower condition. Beach & Bawa (1980) have proposed that such a switch from distyly to dioecism is most likely the result of a form of pollinator-mediated selection for femaleness in the long-style and maleness in the short-style form. In *Coussarea talamancana* Standley (Rubiaceae), the evolution of dioecism is probably the result of a switch in the pollinating fauna from moths that are the characteristic pollinators of the genus *Coussarea* in Costa Rica, to short-tongued bees that are incapable of reaching the lower floral organs (short-styles and short-stamens). Lloyd (1979b) and Beach & Bawa (1980) discuss additional genetic and ecological features of the evolution of dioecism from distyly.

Protandry and Protogyny.—The terms *protandry* and *protogyny* have been used at the level of the individual, for example, to describe changes in sex expression between reproductive seasons in perennial monoecious plants (Frankel & Galun, 1977). In contrast, the terms are conventionally reserved by zoologists to describe changes in sex expression that occur only once during the life of an organism (Heath, 1977). Protandry and protogyny are used here with reference to plants that display dichogamy within a single reproductive season and, more specifically, that usually undergo a male-female or female-male transition within a period of a few days, or as little as a few hours. The terms are also applied here with reference to the relative timing of male and female functions within a flower or at most an inflorescence.

Dichogamy is generally assumed to be an adaptation to limit self-pollination and to promote cross-pollination (Müller, 1883; Proctor & Yeo, 1972; but see Onyekwelu & Harper, 1979; Lovett-Doust, 1980). Undoubtedly, differences in the timing of anther dehiscence and stigma receptivity influence the amount of incoming and outgoing pollen. However, if selective pressure for outcrossing was the only factor involved in the evolution of protandry and protogyny, one would expect these systems to occur in almost equal frequencies and to be distributed randomly throughout the flowering plants. But protandry is far more common than protogyny (Burtt, 1977), and, as discussed below, protogyny seems to be largely confined to certain taxonomic groups and pollination modes.

Protandry should be very common in flowering plants for two reasons. First, intrasexual selection or intraspecific competition for mates should promote the dispersal of a plant's pollen before conspecific stigmas have received pollen from other genotypes (see also Webb, 1981). At the same time, selection should favor the receptivity of the stigma when the pollinators have removed pollen from a diverse array of genotypes. On these considerations alone, one may expect protandry to be an almost universal feature of flowering plants, but since this is not the case, the factors that result in the evolution of protogyny will be explored below.

Second, the fact that pollen but not the ovules undergo dispersal makes the conditions for the evolution of protogyny more stringent than those for protandry. Consider, for example, a population consisting of outcrossing individuals in which the hermaphroditic flowers that open on a given day last only for that day (e.g.,

sunrise to sunset). In such a population protogyny can not evolve unless one presumes the pollinators are carrying substantial amounts of pollen from the foraging undertaken in the previous day. However, in the same population all plants can be simultaneously protandrous because the stigmas can be matured later after some pollen has been deposited on the bodies of the pollinators. As the longevity of the flowers increases, the conditions for the evolution of protogyny become less stringent. Thus in hermaphroditic species, protogyny might only evolve when the processes of pollen receipt and pollen donation in a flower are extended over one daylight period. As discussed below, the flowers of many protogynous species indeed do extend beyond one day. Although extensive data on flower longevity for hermaphroditic angiosperms as a whole are lacking, flowers last one day (i.e., one daylight period) in the vast majority of hermaphroditic plants in the tropics. In many of these species almost all pollen is removed within a few hours after anthesis in early morning, but the peak in nectar production is attained in late morning or early afternoon (Frankie et al., 1981; G. W. Frankie & W. Haber, pers. comm.). Presumably pollen in these species is deposited on the stigmas as pollinators continue to forage for several hours after the pollen has been removed. The late deposition of pollen is also indicated by slight exsertion of stigmas in some of these species in late morning. Although direct evidence for protandry is lacking in these species, they certainly are not, and cannot be, protogynous under the given conditions of flower longevity and the pollinator foraging behavior.

The differences between male and female gametes in dispersal imposes an additional requirement to the evolution of protogyny. Because of the reasons outlined above, unlike protandry, the operation of protogyny is dependent upon some plants being in the male and others in the female phase at a given time. This is usually brought about by asynchronous development of flowers and inflorescences, as for example in the species of the Annonaceae, Araceae (Fig. 3), Cyclanthaceae, Moraceae, and Palmae. In other species, for example in *Persea gratissima*, plants are dimorphic with respect to the timing of male and female phases: in one type the flowers in the female stage open in the morning and then close in the afternoon to reopen in the male stage the following afternoon; in the other type the flowers open in the afternoon in the female stage and then in the male stage in the following morning (Stout, 1924).

The evolution of protogyny can be traced to three aspects of pollination biology. First, protogyny has coevolved in conjunction with several specific life-history aspects of pollinators. In many species of Magnoliaceae, Annonaceae, Araceae, Cyclanthaceae, and Palmae (among others), protogyny is associated with cantharophily (Faegri & van der Pijl, 1971; Bawa & Beach, unpublished observations). The pollinating beetles fly in the late afternoon or early evening to flowers (or inflorescences) while carrying pollen from other conspecific plants and then crawl into some type of enclosure formed by spathes, bracts, or perianth parts and while doing so, deposit pollen on stigmatic regions; after spending the night and most of the following diurnal period in the enclosures, the beetles emerge to fly to another flower or inflorescence usually on a different individual (Fig. 3). Pollen is released just prior to the beetles' departure. The important aspect here is not the pollination by beetles per se, but: (1) the time of beetle flight behavior, (2) the long residency of the pollinators in floral structures, and

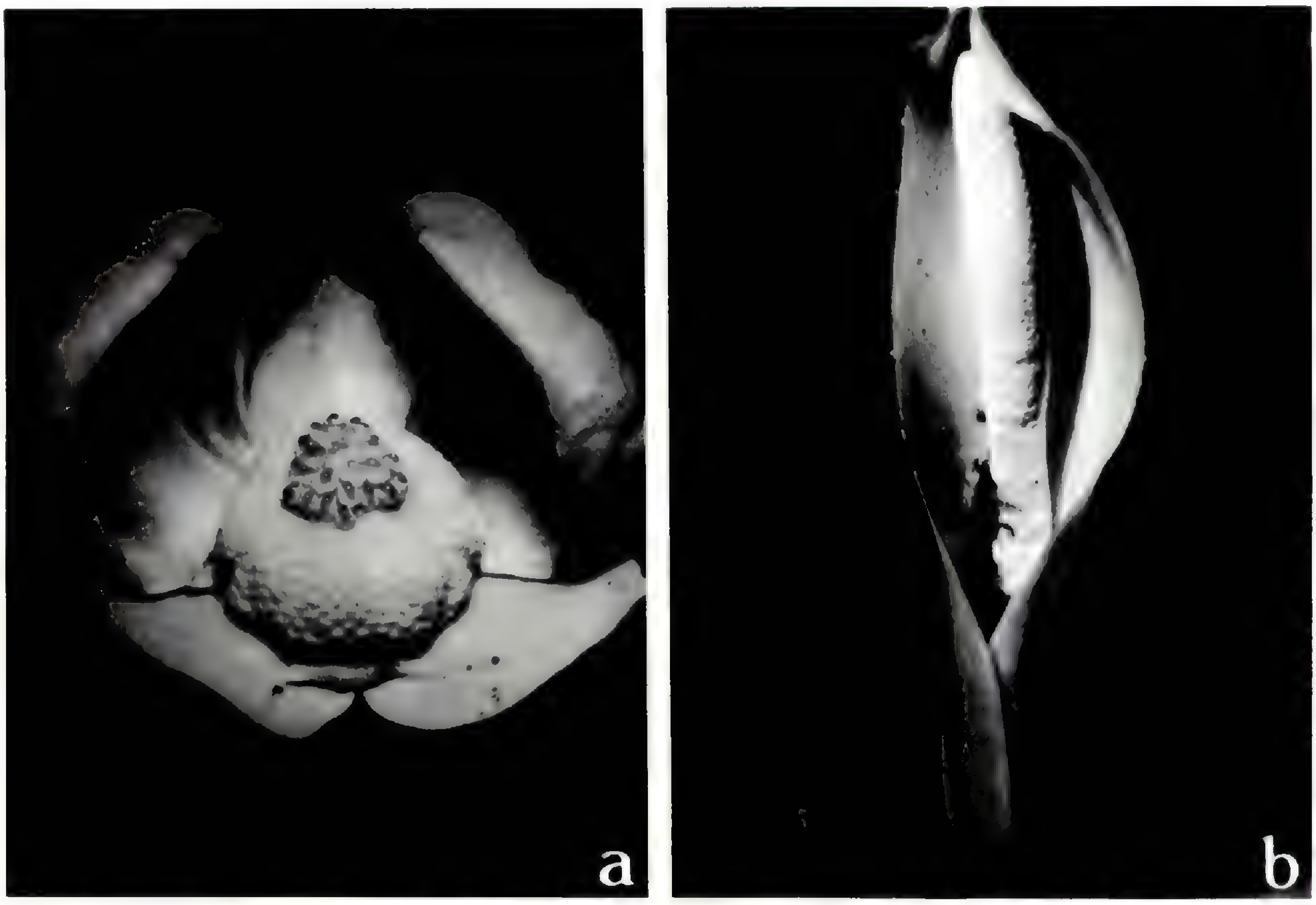

FIGURE 3. Flower of *Cymbopetalum* sp. (a) and an inflorescence of *Dieffenbachia* sp. (b). A petal of the *Cymbopetalum* flower has been removed to show the exudate on the receptive stigmas and the tightly packed stamens surrounding the gynoecium. The inflorescence of *Dieffenbachia* bears female flowers at the bottom, the portion shown to be completely enclosed by the spathe, and male flowers at the top, the portion shown to be exposed. Both the species are from a tropical lowland wet evergreen forest in Costa Rica.

(3) one foraging trip every 24 hours. Recall that in *Ficus*, a genus in which protogyny is an universal feature of the monoecious species, the prolonged inhabitation of wasps is also associated with just one trip between the pollinated and the to-be-pollinated figs (Ramírez, 1969). It is apparent that the type of beetle pollination in the families mentioned above, and pollination by fig wasps could not operate and would not evolve in association with protandry.

Second, selective pressure against the clogging of stigmas by a plant's own pollen may result in the evolution of protogyny. The self-pollen may interfere with the deposition of incoming pollen and/or compete with it for germination sites (Bawa & Opler, 1975). The possibility of clogging increases when the flowers are closely aggregated (Burtt, 1977) and the pollination mechanism is imprecise. There are no observations or data that relate the amount of self-pollen received by the stigma (after the termination of the female phase in protogynous species) to the precision of pollination in either the protogynous or the nonprotogynous taxa. This explanation is different from the traditional explanation that seeks the evolution of protogyny in selective pressures favoring outcrossing, because it removes the difficulty of explaining the occurrence of protogyny in self-incompatible species (see for example Burtt, 1977). Clogging in self-incompatible as well as self-compatible species decreases the amount of incoming pollen that can be deposited on the stigma, as well as the amount of outgoing pollen. Lloyd &

Yates (1981) have used a similar explanation to account for the evolution of protandry in *Wahlenbergia albomarginata*.

Third, uncertainty of cross-pollination may also select for protogyny. Pollen from the anthers of the same flower could be used for pollination if the initial effort in securing cross-pollination were to fail. Protandry may offer no such possibility. It is notable that protogyny is quite common among herbaceous plants that flower early in spring in the north temperate zone, when the conditions for cross-pollination are unpredictable (Schemske et al., 1978).

The consideration of the evolution of protandry and protogyny is complicated by the fact that the plants can be protandrous at the level of the individual and protogynous at the level of flowers and inflorescences or vice versa. For example, most species in the Umbelliferae are protandrous, and the species in which protogyny has been reported have the first order umbels consisting only or mostly of male flowers (Bell & Lindsey, 1978). Thus the so-called protogynous species are, in most cases, actually protandrous. From the evolutionary viewpoint it is the individual-level phenomena that are of interest. However, our phenological knowledge of differential maturation of male and female parts is in most cases restricted to flowers or inflorescences.

Sexually Dimorphic Systems

Dioecism.—Dioecism is widespread in flowering plants. Many attempts have been made to explain its evolutionary basis, and until recently, most evolutionary models have dealt with the genetic benefits of outcrossing as the selective force of most importance (Charlesworth & Charlesworth, 1978; Maynard Smith, 1978; and references therein). Although there is some empirical evidence to support the outcrossing argument (Lloyd, 1981), several alternative models to explain the evolution of dioecism have been proposed (Charnov et al., 1976; Charnov, 1979; Willson, 1979; Bawa, 1980a; Givnish, 1980; Beach, 1981). We will not review all of these recently published proposals, but rather briefly examine those models that deal with the consequences of pollinator foraging behavior on the evolution of the sexual systems.

Most dioecious plants are insect pollinated (Bawa, 1980a), although in the north temperate zone there seems to be an association between dioecism and wind pollination (Freeman et al., 1980). Among the zoophilous taxa, an unusually large number of species are pollinated by small bees or flies (Bawa & Opler, 1975). This correlation between dioecism and pollination by small insects occurs at the taxonomic as well as at the community level of organization (Bawa, 1980a). Three attempts have been made to elucidate the ecological and evolutionary basis of this correlation.

According to Givnish (1980) pollination by small opportunistic insects is inefficient in the sense that they mediate little interplant movement of pollen. Thus, increases in male reproductive effort (in originally hermaphroditic plants) do not result in corresponding increases in paternal fitness. In contrast, Givnish argues that an increase in maternal reproductive investment (e.g., the maturation of more fruits) should result in a disproportionate gain in female fitness. As a consequence, he proposes that female individuals could successfully invade an hermaphroditic

population, and then create conditions favorable for the evolution and establishment of males.

Bawa (1980a) and Beach (1981) have argued that pollinators such as small generalist bees respond dramatically to changes in floral displays. Thus an increase in flower number on an hermaphrodite may lead to a disproportionate increase in male fitness because plants with larger floral displays may either attract more pollinators and thereby disperse more pollen, or be visited earlier in the day and thereby transmit more genes via pollen than via ovules. The variation in flower number may result from intrasexual competition or may be a part of the normal variation in a natural outcrossing population. As a consequence of this variation and the type of pollinator-mediated selection described here, males would be established. Females may become established when individuals with a smaller number of flowers increase their fitness due to resources saved from reduced pollen dispersal costs (see Bawa, 1980a, for other factors leading to the establishment of females).

Lloyd (1981) has suggested that dioecism is more likely to arise in species serviced by small promiscuous insects because pollination by such pollinators would result in a high level of selfing in self-compatible species.

Regardless of which factor has contributed more to the observed correlation, the involvement of pollinators in the evolution of dioecism cannot be denied.

Gynodioecism.—The evolution of gynodioecism involves the establishment of male-sterile mutants in a population consisting of hermaphrodites. There is evidence that selective pressure for outcrossing is responsible for the spread of such mutants (Lloyd, 1981, and references therein). Thus, at this time, pollinator-mediated selection cannot be invoked to explain the evolution of gynodioecism, though it is noteworthy that the majority of gynodioecious species are also pollinated by small insects (D. G. Lloyd, pers. comm.).

Gynodioecism usually evolves into dioecism by the gradual loss of female fertility of the hermaphrodites (Lloyd, 1975a; Charlesworth & Charlesworth, 1978). Selective pressures underlying the conversion of hermaphrodites into males are not fully understood; however, according to Charlesworth & Charlesworth (1978), an increase in pollen production is a requirement. If production were equated with dispersal, increased dispersal could result from pollinator-mediated intrasexual competition for the females, especially if the gain in fitness from increased dispersal outweighed the loss of fitness due to the elimination of female functions. It is noteworthy that in the Umbelliferae, dioecious species have a higher male/female flower ratio than the gynodioecious species (Webb & Lloyd, 1980). It is possible that an increase in male flower number in dioecious species has resulted from intrasexual competition.

Androdioecism.—The establishment of males in a population consisting of hermaphrodites results in the evolution of androdioecism. It is generally assumed that selective pressure for outcrossing does not result in the evolution of androdioecism because in a selfing population, the ovules of hermaphrodites are not readily available to male plants (Lloyd, 1975a; Charlesworth & Charlesworth, 1978). In the absence of selfing, the pollen production of males must be more than twice that of hermaphrodites in order for androdioecism to evolve. Such a dramatic increase in pollen production (and dispersal) may be possible when

pollination is effected by pollen collecting visitors (see also Ross, 1980). Androdioecism has been reported in some species of *Solanum* (Symon, 1979). The flowers of *Solanum* produce no nectar; pollen is the only reward to pollinators, which are pollen-collecting bees. We would predict that most additional examples of the evolution of dioecism from andromonoecism are likely to be reported from bee-pollinated species.

Discussion

We have shown that the influence of pollinators in the evolution of sexual systems stems from a multitude of interactions between plants and pollinators: (1) ability of pollinators to respond to minor changes in floral resources, thereby altering the patterns of pollen donation and pollen receipt (evolution of dioecism); (2) need in plants to retain structures crucial to the integrity of the pollination system (maintenance of andromonoecism, androdioecism); (3) a single foraging trip by the pollinators to flowers or inflorescences associated with long inhabitation in these structures to find mates, avoid predators, or gather food (evolution of protogyny); (4) interference between pollen removal and pollen receipt in plants with small flowers pollinated by unspecialized insects (evolution of monoecism); and (5) precise deposition of pollen on the long mouth parts of pollinators to promote compatible pollinations (evolution of heterostyly). Although we have cited examples where other factors may have been more important, we do not deny the role of outcrossing in the evolution of sexual systems. Different selective forces may operate at different levels. Selection for outbreeding or for an optimal amount of recombination may explain why plants are cross- or self-fertilized, while sexual selection, including pollinator-mediated selection, may explain why outcrossing is achieved in different ways, or why some species are hermaphroditic, others andromonoecious, monoecious, gynomonoecious, dioecious, gynodioecious, or androdioecious.

We have so far considered only spatial and temporal patterns of floral sexuality. It is, however, worth emphasizing that the evolution of self-compatibility and self-incompatibility too is not independent of pollination events. In several taxa, the evolution of self-compatibility has been traced to the paucity of pollinators due to inclement weather (Hagerup, 1951), competition for pollinators (Levin, 1972), changes in pollinator fauna (W. B. Haber & G. W. Frankie, pers. comm.), and the traplining behavior of pollinators that precludes the necessity for physiological self-incompatibility (W. J. Kress, pers. comm.). Self-incompatibility or the ability to discrimate between self- and cross-pollen has evolved only in angiosperms. The flowering plants are also unique in the sense that only in this group does a large number of diverse pollen genotypes land on the stigma as a result of animal pollination (Mulcahy, 1979). In gymnosperms, for example, very few pollen grains reach the pollination chamber (Stern & Roche, 1974). Fisher (1958: 143) was the first to consider the theoretical significance of discrimination against different pollen genotypes in the context of sexual selection. He cited the work of Jones (1928) on G_3 factors in maize to underscore the fact that the discrimination can also involve pollen from different genotypes within the same species, and is not necessarily restricted to self- versus cross-pollen.

We have argued that the evolution of sexual systems is constrained by the

way the pollinators interact with flowers. But, except in a few instances, we have been unable to predict the type of sexual system that would coevolve with a particular feature of pollination. The tremendous diversity of plant sexual systems and their secondary modifications, the wide variety of pollinators and their diverse behaviors, and the lack of general knowledge about the ecological relationships between sexual systems and pollinators make it difficult to develop a general hypothesis. In addition, we have considered sexual systems within the existing classification, but the classification is based on the morphological description of sexual systems, and is inadequate for several reasons.

First, the purely morphological description masks a considerable amount of quantitative variation within different systems. A number of recent studies (Bawa, 1974; Zapata & Arroyo, 1978; Willson & Price, 1977; Schemske, 1980) have quantitatively demonstrated what has been widely observed in hermaphroditic flowering plants: in many species only a small minority of flowers function to produce seeds and fruits. When traditional sexual system criteria are used to evaluate morphological or intrinsic gender estimates, all these species are classified as hermaphroditic on the basis of potential flower function or preanthesis gender. However, if the actual performance of the flowers is taken into account with estimates of functional gender or effective gender, we must conclude that since most flowers function at most as pollen donors, the sexual system of most hermaphroditic species would be more accurately described as andromonoecious. Thus, when gender estimates which include postfertilization events, or at least the probability of male and female function, are contrasted to prefertilization estimates, we note that the same species could be characterized to have two different systems under the existing classification.

A second inadequacy of our current classification is that it falls short of fully describing the temporal distribution of sexual function in a species. The consideration of the temporal dimension changes the properties of the sexual system deduced from morphological grounds alone. A monoecious plant that matures male flowers first and female flowers several days after the male phase does not have the same sexual system as a plant in which male and female flowers mature more or less at the same time. Furthermore, the plant is neither protandrous in the same way as a plant with hermaphrodite flowers, nor is it dioecious, as such plants are sometimes described in the absence of information concerning the temporal sequence of male and female flowers (Bawa, 1977).

Finally, the morphological classification does not take into account the way the system functions. Faegri & van der Pijl (1971), in discussing such well-known examples as the heads of Compositae, Dipsacaceae, and some Leguminosae, point out that in many cases the morphological differences between flowers and inflorescences are in themselves irrelevant in pollination ecology. More important, in the context of this discussion, these differences can also be irrelevant in the characterization of sexual systems. Consider, for example, the two scarab beetle-pollinated genera, the hermaphroditic *Cymbopetalum* (Annonaceae) and, the monoecious *Dieffenbachia* (Araceae) (Fig. 3). The beetles visit these species in the manner described above under *Protandry and Protogyny*. In brief, incoming beetles bearing pollen from other individuals inhabit the protogynous flowers (*Cymbopetalum*) or inflorescences (*Dieffenbachia*) for about 24 hours and then

after the flower or inflorescence completes the male phase, leave in search of additional plants carrying pollen from the flowers or inflorescences just inhabited. The pistils in the *Cymbopetalum* flowers receive pollen in the same way as the female flowers of the *Dieffenbachia* inflorescence, and similarly the stamens release pollen in the same way as the male flowers of the aroid. Thus, from a functional view the *Cymbopetalum* flower is an analogue of *Dieffenbachia* inflorescence. Current sexual system classification obscures the role of the monecious inflorescence as a functional unit. In such a situation, then, it does not seem particularly useful to debate the selective forces responsible for the retention of primary hermaphroditism or the evolution of monoecism unless the dynamics of the pollination biology are taken into consideration.

We conclude with the following:

1. The sexual systems of species are fundamentally linked to the pollination biology of the plants and in many instances can only be understood within the context of the pollination system. We suggest, therefore, that further theoretical considerations as to the adaptive nature of sexual systems must consider in more detail the reproductive ecology of the plants.

2. The taxonomy of sexual systems is largely determined by the type of gender estimates taken at the level of the individual. Intrinsic gender estimates and those based on morphological appearance are not as valuable as estimates of functional or effective gender for determining how floral sexuality actually functions and similarly for illuminating variation in effective gender between conspecific plants. The documentation of this variation is of great utility for understanding the selective forces and evolutionary pathways of sexual system evolution.

3. The temporal dimension of plant sexuality is greatly underestimated by current classification schemes which are largely based on spatial features of plant gender.

4. The morphological distinction between flowers, inflorescences, and even larger groups of flowers such as the totality of flowers in a tree canopy is maintained for most general purposes, but it must also be realized that these units of attraction and/or function might be irrelevant as far as the pollinators are concerned. Consequently, our sexual-system classification is to an extent arbitrary, as class limits are defined on the basis of morphological features and not on the basis of actual function.

5. Finally, we conclude that viewing plant sexual systems with vague reference to the regulation of genetic recombination is unlikely to account fully for the evolution of sexual systems and that the key to understanding them lies in considering patterns of sexuality as means of optimizing male and female reproductive success in different ways within the constraints imposed by the pollination system.

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ON THE EVOLUTION OF COMPLEX LIFE CYCLES IN PLANTS: A REVIEW AND AN ECOLOGICAL PERSPECTIVE[1]

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ABSTRACT

Complex life cycles and alternation of generations are characteristic of many plants, a diploid sporophyte typically alternating with a haploid gametophyte. The prominence of each generation varies greatly among taxa. Purely phylogenetic or morphogenetic explanations of these differences are unsatisfying, as are those based solely on population fitness. Existing adaptational explanations seek selective advantages in diploidy and in sexual reproduction, but these explanations leave much to be explained—i.e., the existence of asexuality and of haploid organisms. Much of the existing variation in life cycles can be explained by selection on reproductive rates to meet the ecological problems of dispersal, colonization, niche preemption and exploitation, and mate competition. Placement of complex life cycles of plants in an ecological framework will, I hope, encourage specific studies exploring possible adaptive aspects and limitations on the evolution of life cycles in plants with different life histories.

A prominent feature of most textbook introductions to various major groups of plants is the description of reputedly typical life cycles of selected forms. Attention is focused on the alternation of haploid and diploid phases (or generations) of the cycle, the relative "dominance" of one phase or another, the timing of meiosis and fertilization, the occurrence of asexual reproduction, and which phase is the dispersal or resting stage. Most of the available published literature on plant life cycles is directed toward elucidating developmental, morphological or physiological and, finally, phylogenetic patterns. A rather small number of papers (see below) addresses the possible selective advantages or disadvantages of reproducing sexually or asexually, of being haploid or diploid, or of having more than one morphological generation. Here, I use the word *generation* to refer to both the alternating diploid and haploid entities and to any intervening, asexually produced, progenies. So far as I can determine, virtually nothing has been written on the ecology (aside from genetics) of complex life cycles in plants. Several botanical reviewers have claimed that all of the ideas summarized here regarding the ecology and evolution of plant life cycles are "old hat." They should be, perhaps, but no one has shown me evidence that they are. This review is presented in hopes of stimulating discussion and research that include an ecological perspective.

I begin by summarizing some apparently classic life cycles of selected plants (broadly defined to include fungi, but excluding prokaryotes). There follows a review of available hypotheses attempting to explain the evolution of such cycles in plants and a critique of these hypotheses. Finally, I review some of the liter-

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ature on complex life cycles in animals in hopes of unearthing some possible approaches useful in interpreting plant life cycles and close by posing some ecological suggestions about plant life cycles that, I think, provide a useful beginning in understanding the evolution of these cycles.

Life Cycle Patterns in Plants

Plant life cycles are many and varied and there are numerous and divers ways of classifying them (e.g., Chapman & Chapman, 1961; Lindenmayer, 1964; Scott & Ingold, 1955). Although in most major taxa some species have become entirely asexual, it is generally considered that all plants exhibit a fundamental alternation of generations. The basic pattern is a 2N sporophyte (producing spores) alternating with a 1N gametophyte (producing gametes).

Relative dominance of one generation over another can be considered in terms of conspicuousness of "body size" and/or in terms of duration. Because an inconspicuous dormant zygote may persist longer than its ecologically active parent(s), I prefer to use body size as an index of dominance. However, if asexually produced progeny are viewed as part of an extended "evolutionary individual" (Janzen, 1977, 1979a), body size and duration may converge in meaning. [Janzen was challenged by Addicott (1979) specifically for aphids (which are obviously not plants, but the idea is relevant!), in which parthenogenesis does not necessitate invariant offspring identical to the parent. While the point is made that genetic identity of asexual parents and offspring cannot be assumed, this does not alter the general idea that asexually produced young are more similar than those produced sexually and the clone is still the unit of selection (Janzen, 1979b).] Some multicellular organisms have potential for large increases in body size (and may also expand by asexual means); other multicellular organisms and unicellular ones may "substitute" asexual multiplication for an increase in body size and prolong the duration of one or both generations by this means.

I am concerned in this paper mainly with plants in which both sporophyte and gametophyte are active, functioning (i.e., not resting or dormant) organisms at appropriate times of the life cycle. Therefore, algae (such as *Fucus* and most diatoms) that exist primarily as diploids, with meiosis during gametogenesis (as is the case in most animals, except certain Foraminifera that alternate haploid/diploid generations (Grell, 1967; Ghiselin, 1974), are of interest mostly as contrasts. Slime molds, as well as some yeasts and other fungi (Raper, 1966b), exist mainly as diploids. Meiosis produces 1N spores that germinate into swimming cells; these fuse to form a zygote that eventually grows (sometimes several together) into a new organism. The seed plants are diploid-dominant also; the 1N gametophytes are tiny and wholly dependent on the sporophyte. In an ecological sense, although not morphologically or genetically, the seed plants may be considered to lack alternation of generations.

On the other hand, certain plants exist primarily as haploids, with meiosis upon germination of the 2N zygote. Many freshwater green algae, typified by *Chlamydomonas*, have a 2N zygote, often dormant, that meiotically forms vegetative 1N cells, which divide mitotically to form either gametes or more vegetative cells. Among the fungi, most phycomycetes are basically haploid (Burnett, 1976). Two hyphae fuse to form a 2N zygospore, which is a multinucleate resistant

phase. This undergoes meiosis to form spores that grow into the macroscopically visible mold.

Between these two extremes are many plants that function actively in two (usually) phases. The gametophyte is more conspicuous in some, the sporophyte in others, and in a few the generations are similar in conspicuousness.

Most bryophytes are conspicuous as persistent, 1N gametophytes. These form gametes by mitosis, the sperm swims to the egg, which lies in a protective jacket of cells, and the resultant zygote grows into a 2N sporophyte, still attached to the (female) parent gametophyte. The sporophyte, generally less conspicuous than the gametophyte, appears seasonally and produces 1N spores meiotically; these disperse and grow into new gametophytes. The gametophyte is considered to be the independent generation and is longer lived. Vegetative propagation, especially by gametophytes, is apparently common.

The 2N sporophyte of the lower vascular plants is more apparent than the tiny, often subterranean, gametophytes. The sporophyte meiotically produces spores that grow into gametophytes that produce gametes by mitosis. Although in some fern populations (Farrar, 1967) no sporophyte is known to exist, the fern sporophyte typically develops on a small 1N gametophyte, which may eventually disappear. Spores have half the chromosome complement of the sporophyte, but high levels of polyploidy permit, in some species, recombination between duplicated, unlinked loci, which produces varied gametes on a gametophyte from a single spore (Chapman et al., 1979; Lloyd, 1974b).

A third pattern of alternation, occurring in several green, brown, and red algae, involves free-living, multicellular haploid and diploid phases. The phases may be similar in external morphology (isomorphic, as in *Ulva*) or dissimilar (heteromorphic, as in "*Derbesia*" and others) (Bold & Wynne, 1978; Fritsch, 1942; Wynne, 1969; Kung-Chu, 1959; Dube, 1967). Each phase may reproduce asexually, forming more individuals of the same phase. The isomorphic forms may grow side by side on the same rocks, thus apparently occupying the same spatial environment; this seems to be the case for *Ulva*. *Ectocarpus* (a brown alga) is intriguing in that it is reportedly isomorphic in warm seas but appears to have a reduced haploid phase in cold waters (Bell & Woodcock, 1968). *Prasiola stipitata* forms spores in the upper intertidal zone and gametes in the lower zone; curiously, the spores are diploid and the lower portion of the "gametophyte" is also while its upper portion is haploid (Friedmann, 1959).

Red algae have varied and complex life histories that are not well understood (P. S. Dixon, 1973). Some consist of three generations: a haploid phase and two diploid phases, one of which is small and attached to the haploid, followed by a free-living 2N phase that is isomorphic or heteromorphic with the haploid, depending on the species. In others the haploid phase grows on the free diploid, and in still others the free-living diploid seems to be lost altogether, meiotic products from the attached diploids growing directly into a new haploid. Many more variants are likely to occur (e.g., West & Norris, 1966).

The aquatic mold *Allomyces*, unusual among the phycomycetes (Darlington, 1958), has isomorphic generations, the haploid phase or gametophyte producing male and female gametes by mitosis on the same filament. These merge to form a 2N phase that can resist desiccation and may produce more 2N individuals by mitosis or 1N individuals by meiosis.

Ascomycetes and basidiomycetes are unusual; they can exist in two different conditions not defined by chromosome number. The 2N zygote is borne on its parent and is highly ephemeral, immediately forming 1N spores by meiosis. The spores disperse and eventually grow into a new 1N generation of hyphae. These fungi resemble most phycomycetes in that the diploid phase is much reduced. However, two hyphae (of different mating strains) can join together to form binucleate cells; this dikaryotic condition may persist for some time. Nuclear status is technically haploid although the organism possesses a double complement of chromosomes. Thus these fungi exist primarily in a 1N or in a 1N + 1N phase.

In summary: some plants produce gametes meiotically; the 1N generation is invariably much less conspicuous than the 2N generation. Other plants produce gametes mitotically. In some of these the 2N generation is inconspicuous. But in others the diploid generation has a period of growth and becomes "apparent" (sensu Feeny, 1976). The apparency of two generations presumably has an adaptive basis, but just how a functional alternation of generations could be adaptive seems to be largely unexplored. Existing adaptational hypotheses applied to plant life cycles address primarily the evolution of diploidy and the evolution of sex. Furthermore, several nonadaptational hypotheses can be found, although Allsop (1966) suggested that "in general terms, the entire life cycle may represent an evolutionary adaptation . . . ," and Bonner (1965) noted that both phases of the life cycle are undoubtedly adaptive.

EXISTING HYPOTHESES SPECIFIC TO PLANT LIFE CYCLES

(A) PHYLOGENETIC AND MORPHOGENETIC EXPLANATIONS

A general trend in the plant kingdom from dominance of the gametophyte to dominance of the sporophyte is often noted (e.g., Chamberlain, 1935; Fuller, 1955; Bonner, 1965). Even taking into account the branching, nonlinear pathways of plant phylogeny, such trends can only be descriptive. The phylogenetic ideas regarding alternation of generations reviewed by Wahl (1965) and Roe (1975) are largely of historic interest. In any case, explanations for the phylogenetic preeminence of, for instance, the angiosperms, are legion (Mulcahy, 1979; Cavalier-Smith, 1978).

Morphogenetic "explanations" invoke genetic and developmental events as causes of morphological conditions (e.g., Bell, 1979). It is sometimes suggested that the function of sexuality in algae is the formation of resistant stages. Although sex may indeed precede the resistant phase and in some species the two events may have *become* tightly linked, it is absurd to suppose that sexuality evolved so that resistant phases could be formed. Asexual modes of reproduction could equally lead to a resistant, dormant stage and do in some organisms (Blackman, 1974; Drebes, 1977). Haploid and diploid conditions are associated with gametophyte and sporophyte conditions, respectively, and this relationship is sometimes taken to be causal (i.e., ploidy controls phenotype), rather than descriptive and associative, according to Bold & Wynne (1978). Nevertheless, haploid sporophytes are known in some algae (*Ulva*, *Cladophora*, Laminariales) and both haploid and diploid gametophytes occur in *Ectocarpus*. Furthermore, bryophyte

and fern gametophytes and sporophytes can apparently exist in either ploidy level (Watson, 1971; Bold, 1967; Bell & Woodcock, 1968) and bryophyte sporophytes can be induced by wounding the gametophyte (Crum, 1973). However, the reproductive potential of such individuals is not indicated (but see Hoxmark, 1975, on *Ulva*); if they cannot reproduce at a rate competitive with their normal confreres, they must be regarded as ecological "sports." However true such mechanistic links might be, they ultimately cannot provide an evolutionary, adaptational, explanation for life-cycle variations.

(B) Explanations dependent on population fitness

"The evolutionary significance of diploidy to higher organisms resides, therefore, in the greater flexibility which it confers on their populations" (Stebbins, 1960: 213; and see Bonner, 1965). Of necessity, the "selective advantage of evolutionary flexibility" in haploid organisms must then be less (Stebbins, 1960). In this sense, evolutionary flexibility is a population characteristic, not an individual one, and thus an indirect consequence of normal Darwinian selection. Such flexibility may indeed exist, however, but may be best interpreted as a population consequence of individual selection as discussed in (C) below.

Similarly, the flushing of the deleterious genes from a population is a consequence of the expression of a haploid generation. From the point of view of an individual, the loss of some proportion of its genes may seem unnecessarily detrimental, since many of them are deleterious only in the haploid state; if zygote formation followed meiosis with little delay, those "deleterious" genes might even have beneficial effects in the diploid. Furthermore, only genes that are "turned on" in a haploid phase could be affected (Bonner, 1965).

A model for the evolution of sexual reproduction as a repair mechanism (Walker, 1978) possesses some attractive features. However, it depends explicitly on population, not individual, fitness (Williams & Walker, 1978) and is not considered further here (but see Dougherty, 1955; Bernstein et al., 1981).

(C) Adaptational explanations

(1) *Diploidy as an adaptation.*—Generally, diploidy is thought to buffer an individual, in some circumstances at least, from the effects of deleterious mutants and to offer the possibility of heterosis (e.g., Crow & Kimura, 1965; Stebbins, 1960; Raper, 1966a; Raper & Flexer, 1970; refs. in Levin & Funderburg, 1979; Rehfeldt & Lester, 1969). Sexual reproduction by diploids also releases genetic variation immediately; this is not true for haploids, which typically must first make a diploid entity as a means of releasing variation (Ghiselin, 1974). Adams & Hansche (1974) consider that these may be secondary effects that arose through time rather than initial advantages of diploidy. In addition, alternative alleles may switch on or off to deal with a fluctuating environment. Diploidy should therefore prevail in particularly variable, unpredictable, or difficult circumstances. These possibilities often seem to provide a standard "explanation" for the evolution of diploid dominance. They necessitate the assumption that all other patterns must occur in relatively benign environments in which the putatively delicate haploid is not at risk. Lewis & Wolpert (1979) suggest that diploids have spare copies of

all genes, which can be modified for new functions and thus easily expand the genome at a much faster rate than haploids, where an original gene must be duplicated before it can be modified. Diploids can therefore more easily evolve the complex gene control mechanisms that characterize complex multicellular organisms. (Lewis and Wolpert further explain sex as an adaptation that preserves diploidy.) Although diploidy may be a preadaptation that permits (through buffering, etc.) the evolution of complex developmental sequences and complicated organisms, this obviously cannot explain the origin of diploidy (Stebbins, 1960; Cavalier-Smith, 1978).

Cavalier-Smith (1978) made the fascinating suggestion that diploidy in eukaryote life cycles may have evolved when rapid growth is less important or larger cell size and lower growth rates are actually advantageous (see Willson & Burley, in press). The volume of 2N nuclei and cells is commonly twice that of haploids and rates of cell division and development are strongly inversely correlated with DNA content (though other factors can be involved also, Bennett, 1974; Price & Bachmann, 1976; Price et al., 1973). Bennett (1971, 1972, 1974) argued explicitly that short generation times require low nuclear DNA content and that high DNA content necessitates a longer generation time. This idea is likely to be involved with haploid/diploid life cycles (Cavalier-Smith, 1978). Furthermore, 1N cells have higher surface/volume ratios, and enzymes active at the cell surfaces may also contribute to faster haploid growth (Weiss et al., 1975; Adams & Hansche, 1974). Such differences in growth and development are only sometimes apparent when conspecific cells of different ploidy (≥2N) are compared (e.g., D'Amato, 1977; Willson & Burley, in press). However, because there is often variation among conspecific individuals in the amount of DNA, we should not yet reject the notion that alternating generations differing in ploidy may have different growth potential. Evans's (1968) interpretation of Durrant's (1962) experiment on the induction by fertilizer treatments of heritable changes in *Linum* is tantalizing: plants with intermediate amounts of nuclear DNA have very plastic growth responses; when grown in conditions inducing large size, the offspring have increased DNA content. Jones (1975) cited evidence from a grass (*Lolium*) that the frequency of accessory or B chromosomes increased significantly with increasing plant density and competition. Intraspecific, clinal variation in DNA content may occur also in *Picea sitchensis* (Burley, 1965; Mitsche, 1971; Moir & Fox, 1977; Mergen & Thielges, 1967; Sparrow et al., 1972; but see Dhillon et al., 1978) and some other conifers (Mergen & Thielges, 1967; Mitsche, 1968). Geographic variation in frequencies of B chromosomes is not uncommon (e.g., Sparrow et al., 1952; Bosemark et al., 1956a, 1956b; Fröst, 1957; Müntzing, 1957; Teoh & Jones, 1978). It would be interesting to learn if this kind of variability occurs in species with alternating generations.

Although B chromosomes apparently carry no major genes themselves, they can affect gene activity and rates of crossing-over on regular chromosomes (Rees, 1972; Jones, 1975, 1976). Altogether, as little as 10% of the eukaryotic genome may exist as unique-sequence DNA that codes for RNA and functional polypeptides (Jones, 1976); much DNA exists as repetitive sequences (more than 10^6 repeated sequences in some cases (Lewin, 1974) and up to 95% of total nuclear DNA content (Flavell et al., 1974) in B chromosomes or other conditions, some

of which are genetically inactive and even non-Mendelian. The preferential transmission of B chromosomes to functional gamete nuclei in both male and female of several angiosperms (Stebbins, 1971) deserves special attention. Although Stebbins (1966) interpreted certain changes in DNA content in terms of possible genetic consequences (e.g., sequential gene action on long chromosomes, reduction of chromosome number to reduce genetic variability, and stabilizing new genotypes in polyploids), it seems reasonable to consider nongenetic consequences of DNA content as well (see also Hinegardner, 1976; Bennett, 1971, 1972).

(2) *Sex as an adaptation to environmental uncertainty.*—Having a sexual generation may be adaptive to changing conditions (Ghiselin, 1974; Williams, 1975; Emlen, 1973). These authors argue that sex is adaptive when production of a varied progeny enhances reproductive success of the parent. Thus, sexual reproduction should occur where or when the environment is unpredictable. Because sex involves recombination, it often results in a more varied array of offspring, which increases the likelihood that some will be able to successfully cope with environmental changes. Without disputing the possible advantages of sex, which have often been debated, I would like to provisionally accept the notion that sex is adaptive in physically and especially biologically varying environments (Williams, 1975; Levin, 1975; Ghiselin, 1974; Treisman, 1976; Glesener & Tilman, 1978; Warner, 1978; Calow, 1978b; Hamilton, 1980; and others).

The timing of sex is also commonly interpreted in terms of environmental change, imminent or just past. Considering spores to represent sex and recombination, Bonner (1958) says that "the spores, when they emerge, have previously undergone recombination (or do so upon germination)." Bonner, Williams, and Ghiselin all provide examples of asexual generations repeating through benign seasons and a sexual generation intervening when the environment is soon to change or has just done so.

CRITIQUE OF EXISTING ADAPTATIONAL HYPOTHESES

First, the supposed delicacy of 1N entities (relative to those of 2N) is somewhat debatable. In bryophytes and green algae the haploid gametophyte is the persistent form; in some algae, 1N and 2N generations have similar gross morphology and may live side by side. Furthermore, haploid cells in vitro are sometimes less sensitive to stresses (putative mutagens, fungicides) than expected (Metzger-Freed, 1974; Henriques et al., 1977; Upshall et al., 1977). And a growing literature on diploidization and gene silencing in polyploids (e.g., Ferris & Whitt, 1977a, 1977b; Garcia-Olmeda et al., 1978) and differential chromosome elimination (Collins et al., 1978) suggests that buffering functions may not necessarily be central. Conversely, the arbitrary suppression of one X chromosome, possibly as a means of dosage compensation (Lyon, 1974; Monk & Kathuria, 1977; Lucchesi, 1978; Epstein et al., 1978), in female mammals suggests that partial haploidy may not be deleterious. Certain parasitic protozoans reduce their chromosome number by means of zygotic meiosis and restore the 2N quantity of DNA just in time for mitotic gametogenesis (Canning & Morgan, 1975). And haploid males occur regularly in certain groups of rotifers, arachnids, and insects (White,

1973). In fact, the tendency of many organisms, both plant and animal, to protect the (2N) zygote in some way could be interpreted to signal its great vulnerability to assorted environmental hazards (just as resistance of the spore is often interpreted). Even in diploid organisms there is variation in amounts of DNA present (Price, 1976; Cavalier-Smith, 1978), even among conspecific individuals (Jones, 1975).

Second, there is increasing evidence (from insects, Rasch et al., 1977; bryophytes, Longton, 1976; ferns, Klekowski & Baker, 1966; *Ulva*, Hoxmark & Nordby, 1974) that DNA synthesis in originally haploid individuals restores the 2N quantity of DNA (but, of course, not heterozygosity and perhaps not reproductive performance; Hoxmark, 1975).

Third, fitness of isogenic haploid and diploid forms of *Saccharomyces* grown in competition with each other were similar when dosages of enzymes active in the cell interior differed with ploidy. But 1N cells out-competed 2N cells when dosages of surface-active enzymes differed. These experiments suggest no advantage to diploidy per se under these experimental conditions (Adams & Hansche, 1974; Weiss et al., 1975). Cavalier-Smith (1978) argues that haploidy may indeed by favored where rapid growth and development are advantageous. Taken together, such evidence suggests that the perils of haploidy may be minor or, at least, could be avoided in many ways. (It may still be true, of course, that a switch from diploidy to haploidy could be difficult once diploidy is entrenched in a group, because many biological features may then come to depend on the diploid conditions and would be disrupted.)

The timing of reproduction must depend on divers factors differing among populations. The production of variability actually occurs twice in a life cycle characterized by alternation of generations, once when meiosis occurs and again when gametes join to form a zygote (see below). For a sexual generation, mate-finding may be a critical problem to overcome, and physiological changes and special mating structures may entail costs in energy or nutrients (Daly, 1978; Calow, 1978b; Muenchow, 1978; Solbrig, 1979). Biological factors including population density and sex ratio are also potentially relevant. A constellation of factors related to the probability of juvenile survival and/or to costs and risks encountered by reproducing adults must be considered with respect to the timing of any phase of reproduction: the availability of suitable (biotic or abiotic) dispersal agents and of "safe sites" (Harper, 1977) for establishment, the risks of "predation" (or herbivory) on young plants of the next generation, the intensity of competition from ecologically similar species (e.g., Schaffer, 1977), the time required and the resources available for maturation (Boyce, 1979), and so on. Predation risks may be particularly relevant to uni- (or few-) cellular phases subject to capture by size-selective predators. Fungal infection of sori may select against a prolonged season of spore production in *Chondrus crispus* (Prince & Kingsbury, 1973). Therefore, aside from a broad correlation of sex with certain kinds of environmental uncertainty, I conclude that existing explanations for the timing of alternation of generations are probably inadequate.

Furthermore, while existing hypotheses aim at explaining the existence of a sexual or diploid portion of the life cycle, they do not suggest why a free-living haploid phase is sometimes retained. Nor have I found many suggestions in the

botanical literature that help explain the relative body sizes of gametophyte and sporophyte or which phase is the dispersing phase, the resistant phase, or the growing multiplicative stages. To begin answering such questions, I present a selective survey of literature, largely zoological, that bears on the ecology and evolution of complex life cycles. From this I hope to glean suggestions that foster the understanding of complex life cycles in plants.

Complex Life Cycles in Animals

Animal life cycles can be broadly classified into two categories. Simple life cycles are characterized by direct development from young to adult. Simple cycles are found among most vertebrates (except many amphibians and some fishes), anthozoan coelenterates, some free-living flatworms and some annelids, hemimetabolous insects, and a few other invertebrates scattered in many taxa. This is not to say that the niches of young and old individuals might not differ greatly, but the transition is relatively gradual. By analogy, seed plants could be viewed as possessing a simple life cycle, since the gametophytic phase has no life of its own. In contrast, complex life cycles exhibit two (or more) distinct phases with very different ecologies and very different morphologies and behavior. There are two kinds: (1) Every surviving individual passes through each phase. Reproduction usually is performed by one phase of the cycle. Typical examples are the anuran tadpole that metamorphoses into a frog or toad and caterpillars that are transformed into butterflies. Complex life cycles of this sort are characteristic of most major animal phyla except chordates, in which only protochordates, some fishes, and amphibians conform to this pattern. (2) Other animals with complex life cycles, such as aphids, rotifers, and cladocerans, and many parasites, are more similar to the "lower" plants: several asexual generations may be followed by one in which sexual reproduction occurs. Each physiologically defined individual usually exists in only one phase, although sometimes females may switch from asexual to sexual reproduction and back. In any event, reproduction occurs in both phases rather than in one.

Istock's (1967) seminal paper focused on the ecology of complex life cycles, particularly of the first sort, noting that distinct phases of the life cycle are largely independent of each other in terms of morphological and behavioral adaptations but are ecologically dependent in that each furnishes individuals to the other part of the cycle. He argued that changes in adaptation of the different phases of the life cycle are not likely to proceed at equal rates and, as a consequence, one phase will sooner or later be unable to supply the other phase with enough individuals, and the population will gradually spiral to extinction. In short, complex life cycles would seem to be evolutionarily unstable. Istock's dilemma lies in the conflict between ecological rationalization and the palpable fact that complex life cycles are extremely common. Considering just the insects, as many as 85% of the species may have complex life cycles (E. McLeod, pers. comm.), indicating that extensive adaptive radiation may accompany life-cycle complexity—which hardly suggests the brink of extinction.

Slade & Wassersug (1975) later showed that instability is not a necessary feature of complex life cycles. Gill's (1978) study of the red-spotted newt (*No-*

tophthalmus viridescens) indicates that adult reproductive failure is common and a small number of adults can produce enough young to maintain many local populations. This suggests that the ecological dependence of population levels at different phases of the life cycle may be loose and that a good deal of variation in recruitment rates can be tolerated. Furthermore, larval and adult phases can not be evolutionarily independent—the life history pattern is a unit (Strathmann, 1974). Ewing (1977) describes a genetic model for the stable maintenance of cyclic haploid and diploid phases.

Indeed, Slade and Wassersug argue that complex life cycles are adaptive, noting (as had Istock) that seasonal (or other frequent) changes in the environment provide temporary changes in resource abundance upon which creatures may capitalize. Fluctuating environments and/or a colonizing or opportunistic life history (e.g., Lewontin, 1965; Hutchinson, 1951) may select for high reproductive capacity of individual parents and possibly also a life-cycle stage with the capacity to exploit ephemeral resources as a means of increasing parental reproductive output. Furthermore, Slade and Wassersug suggest that a second (or third) life-cycle stage may open new means of dispersal—as a means of reaching new sites of ephemerally available resources. Bryant (1969) also argued for the adaptiveness of complex life cycles in insects, especially in spatially heterogeneous environments.

Some evidence is available to support the idea that complex life cycles are adaptive. I divide a series of examples into two "models" for descriptive purposes and convenience (see also Wilbur, 1980).

THE DISPERSAL MODEL

In effect, adult salamanders are viewed as a dispersal phase of the life cycle, metamorphosis from larva to adult often occurring in larvae that are less successful than other individuals in exploiting the aquatic larval habitat (Wilbur & Collins, 1973) or that happen to live in ephemeral ponds (Rose & Armentrout, 1976). Larval phases seem to be prolonged in areas where the terrestrial environment is unsuitable for adults and when the aquatic environment is free from major predators (Sprules, 1974; Bruce, 1979). Sexual maturity may be reached by individuals with larval morphology. This condition is not necessarily associated with an early achievement of reproductive status and, in fact, may be associated with delayed reproduction (Gould, 1977). Delay can have far-reaching consequences because the age of first reproduction may be a critical factor in determining the rate at which a genotype contributes genes to future generations (Cole, 1954; Lewontin, 1965). Goin et al. (1968) note that salamanders inhabiting permanent waters generally have higher DNA content (and slower growth) than those adapted to exploit temporary pools, a suggestion in line with that of Cavalier-Smith (1978).

The red-spotted newt is unusual in having a tripartite life cycle: the aquatic larva transforms into a terrestrial "eft," which eventually returns to water as an adult. Efts are lacking in populations occupying ponds that are suitable year-round. Efts grow and mature more slowly than fully aquatic individuals (Healy, 1973), so the advantage of having an eft stage must outweigh this potential dis-

advantage. Healy (1975) suggests it may reduce the chance of capture by certain pond predators. Perhaps even more importantly, the eft may be a specific adaptation for the colonization of ponds, particularly beaver ponds, that are geologically temporary—lasting for less time than it takes for a population of newts to saturate it (Gill, 1978).

Some salamanders have lost the free-living larval stage and may fall under the next model. Others have lost the adult, dispersing phase, and the "larva" becomes reproductive. I do not know of any salamanders in which the larval stage is the main disperser, but larvae are often the principal dispersal phase of many aquatic invertebrates, such as tunicates (Ghiselin, 1974), and a number of animal parasites, such as trematodes. Holometabolous insects clearly fit the dispersal model as well, adults commonly being the dispersal phase.

THE RESOURCE-EXPLOITATION MODEL

In contrast to salamanders, reproduction by larval anurans is unknown, and only the tadpole stage is ever deleted from the life cycle. Anuran larvae are highly specialized for feeding and rapid growth, and tadpoles are often found in ephemeral ponds very rich in nutrients (Wassersug, 1974, 1975). The larval stage may be lost by species for which no suitable larval environments are available or if the risks of predation outweigh the advantages of rapid growth (Wilbur, 1980). Similarly, planktonic larval stages of invertebrates are often suppressed if potential larval habitats fluctuate wildly (Calow, 1978a). In this model, one phase of the life cycle is viewed as a means of capitalizing opportunistically on rich resources. It may also have been a means of reducing competition between juveniles and adults. In some cases, such as sessile marine invertebrates, asexual multiplication coloniality may be associated with preemption of space (Jackson, 1977).

In some respects rotifers are similar to anurans but with the addition of asexual multiplication of individuals. Most rotifers reproduce rapidly and asexually through the summer (Birky & Gilbert, 1971) when resources are high and, eventually, a sexual generation (King & Snell, 1977) produces overwintering eggs. Rapid asexual reproduction is considered to be an adaptation of opportunistic species that annually recolonize the ponds and lakes in which they live (Birky & Gilbert, 1971). It is likely that different asexual clones have differing capacities for converting food into offspring, thus exhibiting different rates of increase—with the result that the potential for producing sexual young at the end of the season must differ greatly among genetic lineages (see e.g., Snell, 1979, for rotifers; Shick et al., 1979, for sea anemones; Turkington et al., 1979, and Turkington & Harper, 1979, for seed plants).

A complex life cycle of an aphid is described in some detail in the next three paragraphs, because more ecologically relevant details seem to be available. This case seems to combine elements of both dispersal and resource exploitation (see also Bryant, 1969, on holometabolous insects).

Myzus persicae, an aphid, reproduces parthenogentically through the summer, first on *Prunus* spp. hosts, later and for a longer time on a wide diversity of herbaceous host plants (Newton et al., 1953; van Emden et al., 1969). Reproduction is asexual, although some recombination occurs and offspring are variable

(Addicott, 1979), though perhaps less so than if they were produced sexually. At the end of summer when populations are presumably high, a sexual phase occurs and overwintering, sexually produced, eggs are deposited on *Prunus* hosts. The sexual phase is unusual in that females produce males and winged females. These females return to *Prunus* hosts and asexually produce several wingless daughters that mate with the males. Winged aphids produce fewer and smaller young than wingless morphs (A. F. G. Dixon, 1973) and mature earlier (Davies & Landis, 1951). The sexual grandmothers thus obtain multiple granddaughters, centrally located on the winter host (Gould, 1977).

Changes in the host plant may be advantageous in summer because the nutrient content of *Prunus* leaves drops dramatically (A. F. G. Dixon, 1973) and average aphid fecundity, which is very sensitive to soluble nitrogen availability (van Emden et al., 1969), drops to about $^1/_{22}$ of what it was (Davies & Landis, 1951; van Emden et al., 1969). This suggests that, like tadpoles, the asexual summer aphids on herbaceous host may be a way of exploiting an ephemeral flush of resources. Aphid mortality is high when dispersing to new hosts, but the ephemerality of resources on any one host necessitates dispersal (Kennedy & Stroyan, 1959). A return to *Prunus* in the fall may be less related to the senescence of herbage (since aphids seem to like senescing tissue) than to an early and reliable availability of *Prunus* leafbuds in the spring (B. McPheron, pers. comm.), despite the possibly higher predation there (van Emden et al., 1969; A. F. G. Dixon, 1973). Some populations, in regions with no unfavorable season or no *Prunus*, have entirely asexual reproduction (Broadbent & Heathcote, 1955; Blackman, 1974). Overwintering eggs do not ultimately require sexuality for their production inasmuch as two families closely related to aphids produce resistant eggs asexually (Blackman, 1974). The timing of the sexual phase of the cycle may be related both to high population density at the end of a season of intensive multiplication of individuals and to environmental uncertainty.

Reproduction by parthenogenetic aphids is rapid, not as a result of individual fecundity but of phenomenally rapid maturation (Kennedy & Stroyan, 1959; Gould, 1977). The generations are "telescoped," and each grandmother may contain within her body the embryos for the next two generations of aphid. Gould considers the acceleration of maturation and the rapid turnover of generations to be adaptive in reaching and exploiting ephemeral, patchy resources—it is a way of generating large numbers of dispersing young (e.g., Lewontin, 1965; Cole, 1954) to colonize and exploit new patches (see also Ehrendorfer, 1965). Further advantages of asexual reproduction, commonly discussed for plants, may lie in the possibility of establishment of a single propagule (Ehrendorfer, 1965; Allard, 1965; Baker, 1965, 1967; Lloyd, 1974a, 1974b; Holbrook-Walker & Lloyd, 1973; Singh & Roy, 1977) after disersal has been accomplished—thus enhancing the likelihood of success in dispersal.

This selective survey of complex life cycles and reproductive life histories of animals suggests several ecological principles of possible relevance to plant life cycles. (1) In some instances, all parthenogenetically produced daughters of a single female can be viewed as extensions of that female, in terms of exploiting the environment. (2) Asexual reproduction (in various forms) and high rates of

reproduction may be adaptations for colonization and for outcompeting other colonists for available resources. At least one phase of a complex life cycle may be viewed as a means of exploiting ephemeral resources. (3) A dispersal phase is associated with fluctuating environments as a means of escaping to a more reliable patch or as a colonization strategy, enhancing the survival of the offspring. Whether dispersal or exploitation is more important will depend on the population in question. Clearly, several of these principles could apply to any one kind of organism.

These ecological ideas, taken largely from studies of animal life cycles, and others discussed below, are surely germane to plants. In the next section some of these applications are developed.

Toward an Ecology of Plant Life Cycles

For ease of presentation I have segregated this discussion under headings but do not mean to imply that these pieces are unrelated. Nevertheless, it is possible to argue that various life-history features have *gradually* become associated; that is, they are not intrinsically linked (Drew, 1955).

SEXUAL AND ASEXUAL GENERATIONS

The environmental uncertainty hypothesis seems to be the best available hypothesis for the presence of a sexual generation. What then remains is to explain the persistence of an asexual phase in complex life cycles and the timing of each phase. A series of asexual generations probably can be viewed best as a process of self-multiplication. The successful asexual parent, which is well adapted to its circumstances, produces equally well-adapted young rather than variants, some of which would be adaptively inferior in an unvarying environment. To the extent that some form of recombination may be possible in the asexual phase (as in endomeiosis or automixis in certain insects, White, 1973), or if mutations occur, the progeny may not be completely invariant. (Recombinations among genes of a single individual may be considered sexual processes, but I prefer, in the present context, to label as sexual those reproductive processes that can involve two individuals.)

Asexual reproduction (here used to exclude vegetative propagation by rhizomes, stolons, etc.) can often occur more rapidly and less expensively than sexual (Calow et al., 1979; Congdon et al., 1978; Walker, 1979; Whittier, 1970), although this may not always be true (Lamb & Willey, 1979). Coulter (1914), Scott & Ingold (1955), and Ghiselin (1974) hint that the life cycle might be timed around the period favorable for "vegetative" growth. It is likely, even, that the timing of sex is governed more by the advantages of asexual reproduction during seasons favorable for multiplication than by proximity of sexual reproduction to environmental uncertainty—in short, the advantages of asexual reproduction in suitable seasons could delay sexual reproduction until the end of that period.

The costs of mating will also influence the timing of sex. There is evidence for certain algal species that *increased* light or nutrients may induce sexuality directly or indirectly, which hints at resource limitation of sexual activity for

those species (Coleman, 1962; Sager & Granick, 1954). Added carbon sources facilitate production of apogamous sporophytes (not from a fertilized egg) in *Pteridium* ferns (Whittier, 1964; Bell, 1979); could similar effects be found for sexually produced sporophytes? Most experiments in induction of sexual activity in plants have been concerned with proximate triggers rather than nutritive condition of the plants that might determine receptivity to those stimuli. We need to know why particular stimuli (such as N depletion) are appropriate signals to certain species and how the receptivity varies with condition of the organism.

Asexual reproduction is probably adaptive in colonizing and in exploiting ephemeral, patchy resources. Burnett (1976: 550) briefly mentions this possibility of fungi, as does Robinson (1967: 29) for parasitic basidiomycetes. The life histories of many freshwater green algae would seem to conform to this pattern.

HAPLOID AND DIPLOID GENERATIONS

By analogy with animals possessing complex life cycles, it seems likely that gametophytes and sporophytes (as well as asexual and sexual generations) tend to occupy different environments. White (1973: 751) says that alternation of generations *presupposes* two alternative ecological niches. How the niches for plants might differ seems less evident than for animals, in which habitats and/or resources are distinct, but that obviously does not mean that niche differences do not exist. Spatial differentiation of gametophytes and sporophytes is not evident in *Ulva*, bryophytes, or some ferns, but some seasonal or physiological segregation would be possible, as may be true for *Ectocarpus* (Chapman & Chapman, 1973), *Cladophora* (Fritsch, 1935), *Batrachospermum/Audoninella*, and others (Bold & Wynne, 1978: 486). Lubchenco & Cubit (1980) relate heteromorphic phases to herbivory pressures, upright stages accomplishing high rates of growth and reproduction in the absence of predation and crustose stages surviving periods of heavy grazing. However, such morphological differences are not always associated with differences in ploidy and can sometimes be induced by the physical environment (e.g., *Saccorhiza polyscides*, Norton, 1969).

The red alga *Chondrus crispus* is relatively well studied; it apparently exhibits extraordinary variability in seasonal patterns of reproduction by each isomorphic generation, both regionally and between habitats (Prince & Kingsbury, 1973; Mathieson & Burns, 1975; Chen & McLachlan, 1972; Taylor & Chen, 1973; Mathieson & Prince, 1973; Hehre & Mathieson, 1970). Such variability could provide an excellent system for exploring possible adaptive values of seasonal patterns. Unlike the kelps and *Postelsia*, which depend on seasonally opened patches for settlement (see below), *Chondrus* spores settle in quiet microsites protected by other plants (Prince & Kingsbury, 1973) and maturation may be slow (Chen & McLachlan, 1972; Mathieson & Burns, 1975).

Strong seasonal patterns of reproduction (e.g., Longton & Greene, 1969; Tallis, 1959) and marked seasonal differences in sporophyte production (e.g., Greene, 1960; Jones, 1947; Arnell, 1905) are known among many groups of closely related mosses, for example, although the ecological basis for such patterns seems to be unstudied. Ecological comparisons of such species might well elucidate the adaptive basis of seasonal differences in reproductive schedules and the timing of each generation.

If niche differences between gametophyte and sporophyte indeed exist, we can begin to search for possible advantages accruing from the exploitation of different environments. The "models" derived from animals suggest that two likely factors are resource exploitation and dispersal. However, the question still remains as to why it is often entities of different ploidy levels that serve different functions and why, instead, plants with complex life cycles have not evolved, for instance, a 2N "larva" to exploit certain conditions. In fact, it seems that a few algae do exhibit heteromorphic juvenile forms that transform, without a reproductive event, into the adult of that generation (Fritsch, 1942; Allsop, 1966). But the existence of such forms only changes the question to why are they not more common. In short, the possible existence of niche differences does not explain why those niches are often exploited by a haploid and a diploid generation. (In some cases of heteromorphic life cycles, ploidy levels are not regularly associated with a particular morph; Lubchenco & Cubit, 1980.)

Haploids can commonly grow and multiply (asexually) faster than diploids (Cavalier-Smith, 1978; Adams & Hansche, 1974; Weiss et al., 1975), owing to their smaller volume and relatively greater surface area. Therefore they may be suitable entities whenever rapid multiplication is advantageous. If food or space resources are limiting, selection may favor rapid multiplication as a means of preempting the resource and outcompeting lineages that multiply more slowly (see also Cohen, 1977). Such a tactic can be advantageous only up to the point where sibling competition outweighs nonsibling competition. Two factors may alleviate sibling competition: (1) Siblings disperse before sibling competition becomes too intense. (2) Siblings can sequester resources and keep them from other sibling groups. Then if sibling competition becomes intense, death of some siblings might release enough resources that the success of remaining siblings is compensatingly enhanced. Rapid multiplication may also be advantageous if the season suitable for multiplication is short but selection favors production of large progenies. Many offspring improve the success of dispersal (see below). Finally, if there is competition for the privilege of participating in fertilization, there is selection for being well represented in the gamete pool at the time that fertilization occurs. If haploids can replicate faster than diploids (either for intrinsic reasons such as cell size or because the environment they exploit permits them to do so), then a haploid generation may be an evolutionary means of generating numerous gametes to increase the probability that the diploid of one generation will be the parent of many diploids in the next generation. In this case loss of genes that are deleterious in the haploid state may be more than compensated, particularly if release from sibling competition among the haploids allows the remainder to multiply still more.

Diploidy is generally considered to have evolved after haploidy, and therefore it might be thought that the only thing to be explained is diploidy itself. As we have seen, there exist several suggestions about the origin and maintenance of diploidy; the other side of the question is, why retain the haploid? Furthermore, even if haploidy were the primitive condition, it does not follow that extant organisms were originally haploid and secondarily evolved a diploid generation. Diploidy is well established in most major algal groups and goes hand-in-hand with the condition of eukaryosis (Raper & Flexer, 1970). What needs to be ex-

plained *here* is not so much the existence of the diploid, but rather the balance between haploid and diploid phases. Differences in potential growth rates of the two phases seem a likely basis for differential niche exploitation. To the extent that cells modify their DNA content and nuclear size (Jones, 1975; Cavalier-Smith, 1978), such differences may be either decreased or increased.

The peculiar institutions of prolonged dikaryosis or heterokaryosis found among the fungi attracts special consideration (e.g., Raper, 1966b). In a number of species the dikaryon or heterokaryon grows vegetatively, independent of the haploid phase. In many smuts and some yeasts, the dikaryon is not only well developed and long lasting, it has quite different nutritional requirements and/or host specificity than the haploid phase (Raper, 1966b). Thus niche differences are clear. However, the functional significance (in terms of evolutionary adaptation) of dikaryosis compared to true diploidy seems unclear, and Raper (1971) calls them "functional substitutes." Furthermore, many asexual fungi recombine somatically in the dikaryotic phase, forming haploid recombinant products similar to those of sexual reproduction (Raper, 1966b). However, although the genes of dikaryons may usually be expressed as if they were truly diploid and the genes of one nucleus may often compensate for a deficiency in the other (e.g., Medina, 1977), such complementation is not always observed (e.g., Fincham et al., 1979; Lewis & Vakeria, 1977; Medina, 1977; Senathirajah & Lewis, 1975; Roberts, 1964; Pontecorvo, 1963). Darlington (1958) suggests that dikaryosis reduces the costs of reproduction by permitting one fully developed mycelium to fertilize another; the invading nucleus divides upon entry and its descendants move along the receiving mycelium, so that the whole mycelium becomes dikaryotic from a single fertilization event. Furthermore, the genetic character of the dikaryotic mycelium, at least in Ascomycetes, can adjust directly to environmental changes (often created by its own activities; Burnett, 1976) by differentially changing the relative numbers of each type of nucleus (Darlington, 1958). Selection may favor small size of nuclei (and thus 1N) to facilitate division and movement along the hypha (Cavalier-Smith, 1978).

In addition, there is some evidence from several basidiomycetes that dikaryons can grow faster (in the lab) than their uninucleate forms (e.g., Croft & Simchen, 1965; Simchen & Jinks, 1964). A rapidly expanding, dikaryotic mycelium might be advantageous in reaching and preempting such substrates as lignin (B. Benner, pers. comm.). Many basidiomycetes, including these, feed on lignin (Webster, 1970), which persists in the forest soil for a long time and is relatively common (Robinson, 1967). The sugar and cellulose substrates commonly used by other fungi are more ephemeral than lignin, and these fungi have contrasting adaptations that emphasize rapid dispersal and waiting for the resource to become available (Robinson, 1967). However, how general is the occurrence of faster growth rates, and whether (and how) the dikaryotic condition *itself* is the factor responsible, seem to be unknown.

An intriguing but unexplored possiblity is that of conflict between the nuclei of heterokaryons. G. C. Williams reminds me that the interests of the nuclei from two different sources may differ, and it is conceivable that one nucleus competes with the other for resources. A winning nucleus could replicate faster and come to dominate the hypha and perhaps future reproduction in that heterokaryote.

Mechanisms such as synchrony of nuclear division would keep such "cheating" from occurring; but the control of synchrony and its adaptive function need to be elucidated. The persistance of dikaryotic states in the face of such potentially destabilizing tendencies deserves attention.

DISPERSAL

Either the haploid or the diploid phase, or both, may disperse. The 1N stage disperses in many lower plants, although it is the 2N phase in *Fucus* and both in some green algae. The diploid phase is dispersed in seed plants and in animals. (For purposes of this essay, I am excluding pollen dispersal for seed plants because that is not directly involved with establishment of a new individual.) I suspect that dispersal occurs whenever in the cycle it is possible and expedient. Expediency is controlled by a variety of factors, including the availability of proper currents or other vectors that aid dispersal and the presence of suitable safe sites for colonization (Armstrong, 1976). Typically, the dispersal state occupies more continuous habitat than the establisher, whose habitat is often patchy.

A good example may be provided by the kelps (S. E. Franson, pers. comm.), which release their spores in winter, when storms create new openings for establishment in the rocky subtidal zone (Dayton, 1975). The tiny gametophytes can settle in these sites, claiming them for the far larger sporophytes that grow, initially, on the parent and later take its place. The annual brown alga *Postelsia palmaeformis* also depends on continual re-creation of new habitat openings for survival (Paine, 1979). The first sporophytes germinate in February and March, when colonization sites are most available, and grow rapidly, partly as an escape from grazing by chitons (Paine, 1979). Spores are produced through the summer and usually settle near the parent. Short-distance dispersal coupled with an unusual ability of this alga to clear substrate and make it available for its later siblings is apparently a means for this alga to preempt space and thus to maintain the colony through time (Dayton, 1973).

Dispersal is typically a high-risk tactic for colonization—a shotgun search for safe sites (see Hamilton & May, 1977; Strathmann, 1974); because mortality of dispersing propagules is likely to be high, large numbers of such units are commonly produced (e.g., Kennedy, 1975; Ehrendorfer, 1965). The greater the advantage of large numbers, the smaller each propagule may be (to some limit) (see e.g., Smith & Fretwell, 1974). This means that dispersal should usually be preceded by a multiplicative phase, particularly one of high fecundity. In some cases, as in many animal parasites, fecundity is enhanced by asexual reproduction of "larvae," as an adaptation to the uncertainties of dispersal (Kennedy, 1975). Larval reproduction exploits resources not directly available to the parent and thus effectively increases the parental fecundity. The life histories and dispersal ecologies of many green algae and mosses with unusual distributions of habitats may exhibit especially strong selection for high fecundity [e.g., algae saprophytic on nitrogenous wastes or oozing tree sap, or those colonizing the backs of turtles (Prescott, 1968) or sloths, and mosses that specialize to areas burned by hot, slow fires (Southron, 1976) or to the dung of herbivores or carnivores (Crum, 1973)].

However, if these species use sit-and-wait tactics, with long dormancies of the dispersing propagules, the effects on fecundity should be smaller. The astronomical differences in spore production of different mosses—differing by as much as 8×10^7 (Crum, 1973)—are surely related to the probability of juvenile survival and availability of safe sites. Dispersing propagules tend to be small, although spore size in closely related ferns is related to ploidy levels (Walker, 1979), and apogamous fern spores tend to be fewer and larger than those of allied sexual species (Bell, 1979).

RELATIVE DOMINANCE OF THE GENERATIONS

For purposes of discussion, I deal first with multicellular plants that have the evolutionary potential for significant increases in body size of the physiologically defined individual. Typically we find a contrast in body size of the larger parent and the smaller, dispersing offspring. Dispersal units tend to be small, not only because offspring are usually initially smaller than their parent, but for several ecological reasons.

First, to the extent that the success of dispersal is enhanced by production of numerous propagules, the parental resources available for reproduction should be divided as finely as possible, consistent with other constraints on propagule size. Second, they may be carried about more easily by currents or other vectors. Third, perhaps they may have more potentially suitable safe sites in which to land and become established.

Fecundity is often broadly correlated with body size, larger bodies producing more young than smaller ones of the same species; this is true for many invertebrates, fishes, amphibians, reptiles, and even mammals, as well as many seed plants (e.g., Werner, 1975; Leverich & Levin, 1979; Harper & White, 1974). Not only can large bodies often capture more nutrients, perhaps having a competitive edge over other plants (Grime, 1977), they can also structurally carry more offspring (e.g., Calow, 1978b). *Fucus vesiculosus*, for example, has a minimum size for reproduction; if that minimum is not reached in time for the sexual season, sexual reproduction is delayed until the following season. Large plants can bear over 3200 receptacles for egg development. Juvenile mortality is very high, due to washing away and mollusc grazing; adults may live as much as 4–5 years in sheltered locations (Knight & Parke, 1950). Selection for production of numerous offspring is presumably strong, the reproductive season is long, and body size clearly affects "litter" size.

In addition, the very small gametophyte of some leptosporangiate ferns may have eliminated production of multiple zygotes and multiple sporophytes (Buchholz, 1922), potentially reducing both total output and the means available to a female of choosing among potential fathers for her offspring.

So we might predict that large body size ("dominance") may be characteristic of the life-cycle generation subject to the greater intensity of selection for high fecundity (and capturing resources). This could be the generation that precedes the dispersal phase and/or the one whose offspring begin exploitation and preemption of an ephemeral environmental patch. At the same time, there is likely to be a cost associated with growth (e.g., in terms of increased risk of mortality; Sarukhán, 1977), which is one source of limitation on the achievement of large body

size. Other limits on achieving a large body size exist (Littler & Littler, 1980) and include grazing pressure (Lubchenco & Cubit, 1980).

Other reproductive functions may also affect body size. The height of the sporophyte in mosses and the lower vascular plants often increases greatly at maturity (Crum, 1973) and may increase dispersal potential of the airborne spores (Coulter, 1914). On the other hand, gametophytes may be most successful if small, thereby increasing access to water for gamete movement (Coulter, 1914). Given that the sporophyte is borne by the gametophyte, rather than vice versa, perhaps for the above reasons, in mosses another factor may be involved. The moss sporophyte is supported and often nourished by the gametophyte (Thomas et al., 1978; Bell & Woodcock, 1968; Crum, 1973; but compare Bold, 1940). Physiological dependence of sporophyte on gametophyte suggests that bryophytes may often have difficulty in getting enough "food." Even though many sporophytes are independent in terms of carbon supply (Bold, 1940), much nutrition is apparently garnered by gametophyte leaves (Watson, 1971; Tamm, 1964; Clymo, 1963) and gametophyte growth is seemingly correlated with moisture availability (Pitkin, 1975; Tallis, 1959). A conspicuous gametophyte is probably a means of feeding a growing sporophyte; a striking reduction of gametophyte size in mosses, such as *Ephemerum* (Crum, 1973), and some ferns (Lloyd, 1974a) may indicate that nutrient capture is less critical than claiming a site for settlement. Finally, the risk of damage by herbivores may vary with size, and change in size is one evolutionary means of reducing such risks.

For unicellular plants (and others with strict size limitations on physiological individuals), the fecundity and nutrient capture arguments may be germane from the viewpoint of evolutionary individuals. Even though body size of physiological individuals remains small, high fecundity and resource acquisition may be achieved through asexual multiplication (especially of haploids?). A limit may be placed on the extent of such multiplication if local sibling competition reduces the reproductive ability of each individual.

Body size and fecundity also have potential effects on the generation of variable offspring through sexual reproduction. If meiosis follows fertilization without intervening cell division, as happens in many algae (Round, 1973; Fritsch, 1945), only two possible recombinations can be realized (Svedelius, 1929). The more cells are dividing meiotically (up to a point), the closer the theoretical maximum number of variants can be approached (see also Ghiselin, 1974: 72; Burnett, 1976: 550). This argument was also presented for red algae by Searles (1980). Thus, physiological individuals producing large litters and evolutionary individuals that achieve the same fecundity in different ways both generate variable progenies. For species with both sporophyte and gametophyte generations, variability is produced at two points in the cycle (neglecting somatic mutations and recombinations), when meiosis produces segregant combinations and when those join in new combinations to form a zygote (Ghiselin, 1974).

Conclusion

The interpretation of plant life cycles as ecological "strategies" remains unsatisfactorily general and incomplete for many reasons. I have suggested that complex life cycles may be adaptive in dispersal and colonization, in competitive

interactions and resource preemption, in competition for mating privileges, and in increasing fecundity to increase the likelihood of success in the first three endeavors. By calling attention to some likely kinds of interpretations, I hope to encourage both tests of these ideas and the generation of new and more specific ecological hypotheses relevant to complex life cycles in plants. The incredible array of life cycle variants seems bound to be linked to an equally fascinating variety of ecological conditions—an array perhaps unmatched in animals.

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FLORAL REWARDS: ALTERNATIVES TO POLLEN AND NECTAR[1]

BERYL B. SIMPSON[2] AND JOHN L. NEFF[3]

ABSTRACT

In angiosperms selection has led to the utilization of numerous substances other than pollen and nectar that help to insure repeated visitation by pollinating animals. Here, we group the various substances into nonnutritive and nutritive rewards and discuss within each group the specific kinds that occur. In our discussion of nutritive rewards, we emphasize floral oils, lipids produced by one of two types of specialized secretory organs called elaiophores and which serve as nutritive rewards for certain New World anthophorine bees. Although discovered only within the last 15 years, the syndrome of oil production now appears to be one of the most widespread kinds of floral rewards. We report here for the first time the occurrence of oil production in the Solanaceae (*Nierembergia*). It is apparent that oil production has evolved independently many times, but plants which produce oils that are collected by female anthophorine bees show similarities in the chemistry of the oils and the types of structures that produce them. It is not clear whether other groups of plants reported to produce oils but which are not pollinated by anthophorine bees possess an analogous system or not.

Floral rewards can be considered any component of a flower or inflorescence that is used by animals and, because of this use, insures repeated visitation that will lead to pollination. Without doubt, pollen and nectar are the primary rewards offered by flowers to visiting animals in order to buy their services as pollinating agents. Of the two, nectar is sought by a wider array of animals than pollen. On the other hand, pollen is the primary reward for which bees, probably the single most important group of pollinators, visit flowers. The role of pollen and nectar in the attraction of potential pollinators has been appreciated for hundreds of years, but we have only recently begun to realize the complex nature of these two rewards. Nectar, for example, formerly considered to be a simple sugar solution, has been shown to consist of a variety of chemicals dissolved, or suspended, in an aqueous solution. These range from mixtures of one to three common sugars (glucose, sucrose and fructose) to more complex sugar solutions (Percival, 1961) or combinations of sugars, free amino acids, "vitamins," lipids, and other compounds (Baker & Baker, 1975; Baker, 1978). The complex chemical nature of pollen has been realized for a century (refs. in Barbier, 1971), but only in the last twenty years have researchers begun to explore the varied nature of specific enzymes contained in the pollen walls and their possible roles in incompatibility reactions (Stanley & Linskens, 1974). These same enzymes may play a role in pollen recognition by specific pollinators. The chemistry of pollen is in fact so complex that it has been impossible to provide a precise description of pollen chemistry that is all-inclusive. The continued elucidations of the intricate nature of these common rewards has spurred studies of pollination biology and provided an impetus for the investigation or reinvestigation of other floral rewards.

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TABLE 1. Floral rewards other than nuptual nectar and functional pollen.

Nonnutritive rewards
Incidental by-products of floral structure
Floral trichomes used in nest construction
Sleeping places
Heat sources
Mating sites
Products actively secreted as rewards for potential pollinators
Nest materials (resins, waxes, or chemical mixtures)
Sexual attractants
Nutritive rewards
Brood places (larval nutrition)
Adult nutrition
Food tissues (food scales, food bodies, sweet tissues, pseudopollen)
Nonfertile "food" pollen
Stigmatic secretions
Fatty oils (lipids)

Here we will concentrate on floral rewards other than nectar and pollen in the traditional senses of pollen as functional gametes and nectar as a primarily sugar-dominated water solution secreted from one of the numerous kinds of floral nectaries (Fahn, 1952, 1979; Kartashova, 1965). Most of the rewards we discuss have been derived from totally different portions of the flowers or inflorescences, but we will include rewards that have been derived from pollen or nectar but which are now functionally or chemically distinct.

In our discussion, we have divided alternative rewards into two groups. The first group includes those used by pollinators for purposes other than nutrition and the second, those which serve primarily as food sources for adults, larvae, or both. Table 1 lists the kinds of rewards within each of these categories. Of the rewards in the latter group, we will emphasize lipids most heavily, primarily those of the Krameriaceae and Malpighiaceae, groups with which we have been working for several years.

NONNUTRITIVE FLORAL REWARDS

STRUCTURES WHICH SECONDARILY SERVE AS FLORAL REWARDS

Nest Construction.—In several cases animals, primarily insects, visit flowers for something which appears to be unrelated to pollination per se. In other words, the structures used appear to have an adaptive function not directly related to the attraction of pollen vectors. The relationships between the flower and the visitor in these instances is often so casual and/or the probability of pollen transfer so low, that there has been no selection for the enhancement of the association, and consequently no further modification of the structures used. An example of this type of association is the collection of floral trichomes for use in nest construction by some bees. We have observed bees of the genus *Anthidium* visiting *Krameria* and *Larrea* flowers in order to clip trichomes from the surface of the ovaries. The position of the bees indicates that they can effect some pollination while engaging in this activity. Generally, however, these bees use vegetative trichomes, and there appears to be no selection for an increase in the abundance

of ovarian trichomes as a reward to encourage such visitation. Similarly, during the collection of petals or pieces of petals of some flowers, leaf cutter bees occasionally may effect pollination, but the relationship is always a very casual one.

Sleeping Places and Heat Sources.—Flowers, as a result of their shapes and behavior, can be used by either male or female (but primarily by male) bees as sleeping places. In some instances the selection of a particular flower species in which to spend the night is quite rigid; in other cases, any funnel, tube, or dish-shaped flower that closes for the night apparently will do. The use of flowers as sleeping places is quite common, but rarely reported even though the movement into and out of flowers undoubtedly leads to occasional pollination (Linsley et al., 1956; personal observations). Nevertheless, there appears to be no selection for the reinforcement of this relationship, presumably because the females of the species which sleep in the flowers usually collect nectar and/or pollen from open flowers during the day and serve, much more efficiently, as pollinators.

Resembling the use of flowers as sleeping places is their use as "heaters." Particularly in the Arctic and at high elevations where ambient air temperatures are quite low, dish-shaped flowers can collect heat within the bowl and provide energy necessary for insect activity (Hocking & Sharplin, 1965; Kevan, 1972; Smith, 1975). Several researchers have postulated that selection has increased the ability of some flowers to absorb or concentrate heat (Hocking & Sharplin, 1965; Kevan, 1972; Smith, 1975) because they attract insects that can serve as pollinating agents.

SUBSTANCES PRODUCED SPECIFICALLY TO SERVE AS FLORAL REWARDS

Nest Construction.—The production of chemical substances by plants that are gathered by bees for use in nest construction is well known (Krombein, 1967; Grigarick & Stange, 1968; Iwata, 1976). The substances are generally resins exuded from the stems of plants, including conifers, legumes, mangroves, and species of the Euphorbiaceae. These exudates are believed to serve a primary function within the plant as deterrents to predation (Berryman, 1972). A novel case of resin production as a "floral" reward has been recently investigated by Armbruster & Webster (1979) in *Dalechampia* (Euphorbiaceae). Terpenes secreted by glands on the pseudanthium, a highly reduced inflorescence, of several species of the genus (Armbruster, in correspondence), attract female euglossine, anthidiine, and trigonine bees that visit the inflorescences to gather the resin and, while doing so, deposit and pick up pollen. In actuality the secretory gland is a vegetative structure, but the nature of the inflorescence is such that the entire structure with its subtending bracts functions as a flower.

Some species of *Clusia* (Guttiferae) have been reported also to have flowers that secrete a sticky substance collected by bees, presumably for use in nest construction (Armbruster & Webster, 1979; Armbruster, in correspondence). Florally produced waxes of *Maxillaria divaricata, M. veriferum* and *M. flavoviride* (Orchidaceae) collected by female bees as nest-construction material can apparently also serve as pollinator rewards (Porsch, 1905; van der Pijl & Dodson, 1966).

Other cases that may eventually be shown to involve the production of non-

nutritive rewards include Ericaceae that produce concentrations of waxes on the back of the stamens (Dorr, 1980), oily exudates of *Eria vulpina* (Orchidaceae) flowers (Kirchner, 1925), and the secretions of the anthers of *Mouriri* (Melastomataceae, Buchmann, 1978, but see lipids below).

Sexual Attractants.—Deceit, or the trickery of flowers to lure pollinating insects to themselves by mimicking food, brood places, or female insects is not considered here to be an actual reward. In *Ophrys* (Orchidaceae, cf. Bergstrom, 1978), flowers have been shown to produce scents that attract male bees, but they do not appear to provide any actual reward for the individuals which land on, and attempt to copulate with, the flowers. Other plant species, however, produce sexual attractants that are collected in appreciable quantities by pollinating male bees. In these cases the chemicals can be considered true rewards. The most publicized examples of the production of sexual attractants and their collection involve members of the Orchidaceae and euglossine bees (Dodson & Frymire, 1961a, 1961b; Vogel, 1963, 1966a; van der Pijl & Dodson, 1966; Dodson et al., 1969). The oils, now known to be primarily monoterpenes, are collected only by males which land on flowers and brush patches of secretory tissue with hairs on the tarsi of the front legs. The oils are absorbed onto the plumose hairs and then transferred to the hind legs where they diffuse into highly vascularized regions inside the tibia (Vogel, 1963, 1966a). Despite years of investigation, the use of the collected oils has not yet been conclusively proved (cf. Williams, in press, for a thorough review of orchid-euglossine relationships).

After it was established that the male bees were not gnawing on the petals, investigators hypothesized that the oils might contain scents that mimicked odors of females or nests (Vogel, 1966a), but this idea was discounted when it was shown that the bees were collecting chemical substances (Dodson & Frymire, 1961b; Dodson et al., 1969). A second hypothesis proposed by Vogel (1966b) was that the floral oils were used by the male bees in the production of pheromones. Williams (1980, in press) has recently elaborated on this hypothesis and proposed on the basis of preliminary chemical results that the males modify the floral monoterpenes in the legs, transport them within the body, and then again chemically alter the compounds in the mandibular glands. The mandibular gland secretions are species specific pheromones. At the same time that Vogel put forth his second hypothesis, Dodson (1966) suggested that the oils were metabolically important for the male bees and prolonged their lives. This idea is now, however, generally discounted (Williams, in press). A final theory about the use of the oils later proposed by Dodson (1975) was that they were used by specific males to attract other males into leks that subsequently attracted females with which they would mate. While the failure of field researchers to observe leks as a common phenomenon argues against this idea, it has not yet been disproved.

The associations between euglossine bees and orchids is often very precise and appears to be a highly coevolved system involving precise mixtures of floral compounds and very species specific taxa of bees. The syndrome is not, however, limited to the Orchidaceae. The collection of floral scents by male euglossine bees has been reported in the Araceae (*Spathiphyllum*, *Anthurium*, and *Xanthosoma*, Dodson, 1966), Gesneriaceae (*Gloxinia*, Vogel, 1966b; *Drymonia*, Williams, in press), Solanaceae (*Cyphomandra*, Williams, in press), Euphorbiaceae

(*Dalechampia*, Armbruster & Webster, 1979), and Haemodoraceae (*Xiphidium*, Buchmann, 1978, 1980). In *Dalechampia* (Armbruster & Webster, 1979) a somewhat unusual situation pertains in that the oils are produced by a gland on the pseudanthium rather than by a gland within a flower. Williams (in press) also mentions some Cyclanthaceae that may use floral volatile oils as rewards for pollinating insects.

Nutritive Substances

Floral substances consumed by animals that can serve as pollinators range from various kinds of flower tissues to complex secretory products. In our discussion of nutritive floral rewards, we will consider first unspecialized tissues of flowers or inflorescences, then modified tissues, and finally, particular secretory products.

The actual tissues of a flower or an inflorescence can be consumed by animals that play varying roles in the pollination of the plants on which they feed. As in the case of other types of floral reward-pollinator interactions, these associations cover the spectrum from casual encounters to obligately interdependent relationships.

brood places (larval food sources)

We will consider first brood place associations involving tissues that do not appear to have been modified for any particular nutritive function. However, it has been shown that the adults which oviposit in the flowers serve as pollinators while searching for, and ovipositing in, host plants. The larvae themselves rarely effect pollination as they are usually confined to a flower or inflorescence during development and are generally mobile only after the periods of anthesis and stigma receptivity have ended. When we talk of brood place-pollinator relationships, we are not speaking of simple parasitism of flowers and the developing ovules such as occurs with bruchids and legumes (Zacher, 1952) or tephritid flies and species of the Compositae (Christenson & Foote, 1960). While adults of these insect groups are often associated with the flowers of the species on which they oviposit and are usually quite specific in their choice of host plant, they do not constitute significant pollinators in terms of the number of visits per flower per unit time or in terms of amounts of pollen carried from flower to flower. Our use of brood place as a floral reward is restricted to cases in which the adults have been shown to be one of the most important, or the only, pollinator of the flowers involved.

Perhaps the two most famous examples of plants dependent on ovipositing adults as pollinators are the *Yucca* (Agavaceae)—yucca moth (*Tegiticula* spp.) and the *Ficus* (Moraceae)—fig wasp (Blastophagidae) associations. The intricate relationships between these taxa and their pollinators have fascinated botanists for many years and have been described numerous times (e.g., Proctor & Yeo, 1972; Faegri & van der Pijl, 1979). In both cases it is now known that pollen, a traditional floral reward is gathered, but not consumed, by the females of both the yucca moths and fig wasps. In *Yucca* a pollen ball is gathered by a female moth from a flower or series of flowers. She then carries the completed ball to

another flower and begins to oviposit. She usually interrupts the ovipositing process to climb to the top of the style and force the pollen ball into the stigmatic cavity. The larvae which hatch feed on the developing seeds (Riley, 1872; Powell & Mackie, 1966). Unlike the yucca system in which one species of moth pollinates the vast majority of *Yucca* species, figs are pollinated by species-specific female wasps. The tiny females become dusted with pollen (active packing of pollen into pockets on the thorax and coxae also occur in many taxa, Ramírez, 1969) when they leave the synconium in which they developed and mated. After entering a different synconium in search of oviposition sites, these females pollinate numerous flowers. The larvae develop in, and feed on, the ovarian tissues of female fig flowers.

The jackfruit, *Artocarpus heterophyllus* (Artocarpaceae), likewise appears to have adapted to the use of brood-place seeking females as pollinators. Van der Pijl (1953) reported that clusters of male flowers in which females of the genus *Dettopsomvia* (Drosophilidae: Diptera) oviposit are enlarged relative to other members of the genus and provide a medium of floral tissue for larval development. A similar association between flies of the genus *Atherigona* (Anthomyideae: Diptera) and *Alocasia pubera* (Araceae) was also reported by van der Pijl (1953). Other plant species, with perfect rather than unisexual flowers, also use floral tissue as larval food as a reward for pollinating female insects. Thrips that oviposit in flowers have been suggested as the pollinators of different species of *Calluna*, *Phyllode*, and *Erica* (Ericaceae) by Hagerup & Hagerup (1953), but Haslerud's (1974) results indicate that the female insects effect little or no pollination except, perhaps, in *Erica*. In *Trollius europaeus* (Ranunculaceae), larvae of its major pollinator *Chiastochaeta trollii* (Thysanoptera) consume receptacular tissue and developing ovules later in the season (Hagerup & Peterson, 1956). Recently, Brantjes (1976a, 1976b) carefully described the relationship between *Melandrium album* (Caryophyllaceae) and its principal pollinator, female *Hadena bicruris*, a noctuid moth. The females visit the flowers for nectar and to lay their eggs in the receptacle. After hatching, the larvae consume an appreciable portion of the potential seed crop. In this particular case Brantjes concluded that there is a precarious balance between pollinator service and simple seed predation. In *Thuranthos* (Liliaceae) an equally hazardous system exists. The two species of this African genus appear to depend on noctuid moths (i.e., *Diaphone eumela*) for pollination (Stirton, 1976). The adult females, which feed on nectar of open flowers, oviposit on young, unopened buds at the apex of the flowering inflorescences. The developing, voracious larvae crawl down the rachises, consuming ovaries and maturing fruits.

In contrast to plant species which are pollinated primarily by insects feeding on completely unspecialized floral parts, are several taxa that have a proliferation of certain tissues as food sources for the larvae of pollinating insects. These plants are often obligately dependent upon their pollinating-parasitizing visitors. One of the cases in which this sort of syndrome is most dramatically exhibited is in the Hydnoraceae. Both of the genera of this family, *Hydnora* and *Prosopanche* are obligate root parasites of other angiosperms and both appear to depend upon beetles for successful pollination. None of the species of the family has leaves. Flowers and fruits are the only portions of the plants borne above

ground. In *Prosopanche americana*, nitidulid beetles (*Neopocadius nitiduloides*) and weevils (primarily *Oxycorynus hydnorae*) feed as adults first on the outer walls of the perianth and, when the flowers open, on the staminal column inner perianth walls. Once they have crawled into the flowers, the insects become temporarily trapped, but continue feeding and simultaneously oviposit into the inner perianth walls. Occasionally, a female which has arrived dusted with pollen will crawl into the lower chamber of the flower and contact the flat stigmatic surface. The anthers of *Prosopanche* dehisce a day or so after the flower opens, dusting females who have completed oviposition. The insects then crawl or chew their way out of the flower (Simpson & Neff, 1977). During the period of fruit maturation, the larvae of these groups feed on the particularly thick layers of floral parenchyma. Bruch (1923) described a similar sequence involving the same beetles for the second member of the genus, *P. burmeisteri*. *Hydnora*, the other genus in the family, also appears to be pollinated by beetles, but the accounts of both Marloth (1907) and Vogel (1954) indicate that it attracts carrion beetles and flies because of its fetid odor and red-purple color. It is not clear if the white, fatty structure inside the flower described by Marloth (1907) functions simply as a source of an odor attractant, or if it acts as a food body. Similar structures in *Prosopanche americana*, which lack a strong odor, are involved in the floral trap mechanism.

ADULT FOOD SOURCES

While floral or inflorescence tissue may be enlarged for larval nutrition, there appear to be no proved cases in which there is a special type of tissue produced as a source of food for the larvae of potential pollinators. For tissues other than pollen that serve as nutritive rewards for adult animals, this is not the case. The pandanaceous genus *Freycinetia* has fleshy bracts surrounding the flowers. These "food bracts" were initially hypothesized by Porsch (1930) to serve as food for birds and bats. Recently, Cox (1980) has shown that flying foxes feed on the bracts and simultaneously pollinate the flowers of the dioecious plants. Likewise, Baker (1978) reported that the fleshy sepals of male flowers of the palm *Bactris major* are eaten by pollen-carrying beetles, and Purseglove (1968) proposed that the staminodes in cacao flowers (*Theobroma cacao*, Sterculiaceae), are pierced by pollinating certopogonid midges. In several species of Araceae, parts of the spadixes have been modified into food tissues (Faegri & van der Pijl, 1979) that are gnawed by pollinating beetles. These tissues are on the lower part of spadix in *Amorphophallus variabilis* and form projections above the female flowers in *Typhonium trilobatum* (van der Pijl, 1953). A final example is the sweet corolla of *Madhuca* (Sapotaceae) species (Faegri & van der Pijl, 1979).

Beach (in correspondence) has found that species of *Bactris* (Palmae) have glandular trichomes on the inflorescence rachises that are consumed by scarab beetles (*Cyclocephala*) while they mate on, and also pollinate, the flowers.

About thirty years ago, Grant (1950) demonstrated that the flowers of *Calycanthus occidentalis* (Calycanthaceae) are primarily pollinated by a nitidulid beetle (*Coleopterus truncatus*) that feeds on the tepal tips that have become modified into food bodies. McCormack (1975) later demonstrated that many species of beetles are initially attracted to the flowers by a complex array of volatile com-

pounds which may mimic fungal odors, rather than by the food bodies themselves. Rickson's (1979) study of the composition of the food bodies showed that they were rich in protein with low levels of starch and lipids. Starchy food bodies serve as rewards for pollinating beetles in several species of *Nymphaea* (Nymphaeaceae) (review in Schneider, 1979).

In the Orchidaceae a number of cases of specialized food tissues have been reported, but many of these appear to need substantiation. The reports indicate that some orchids have a sugar-rich food tissue that must be pierced in order to obtain the sweet fluids (van der Pijl & Dodson, 1966). The aspect of these cells is similar to that of normal epidermal nectaries, but the nectar is not secreted. Among genera reported to have this type of tissue are *Cattleya, Epidendrum,* and *Sobralia.* In *Diuris* a similar tissue forms a ring on the top of the receptacle (Coleman, 1932). Various workers have indicated that many *Orchis* species may also have a type of tissue that must be pierced to obtain a sweet liquid (Knoll, 1956; van der Pijl & Dodson, 1966), but other investigators have concluded that the spurs of the flowers are empty and attract pollinators only by deceit. Other species of the Orchidaceae have been reported to have trichomes called food hairs that are collected or consumed by pollinating bees. At least two species of *Polystachya* (Porsch, 1906; Beck, 1914) have trichomes on the labellum that have been hypothesized to serve this function. However, Vogel (1978), after observing *P. pobequini,* decided that the trichomes are "empty," of no food value, and serve as pollen mimics rather than as a food source. In *Maxillaria rufescens* studied by Porsch (1905), the floral trichomes were shown to contain starch and lipids. Van der Pijl & Dodson (1966) list several other species of *Maxillaria* for which they indicate they have evidence of food hairs being consumed by pollinating bees. A final purported food tissue in the Orchidaceae reported by Beck (1912) is in the form of food scales on labellum of *Vanilla planifolia* which appear to contain sugars and starches. Van der Pijl & Dodson (1966) also list *Coelogyne* and *Cymbidium* as having scales or hairs that are grazed by bees.

Pseudopollen.—Closely related to food trichomes is pseudopollen. We should mention here that the term pseudopollen has been used in two somewhat different ways. Van der Pijl & Dodson (1966) defined pseudopollen as a pollenlike mass of cells that results from the disintegration of multicellular trichomes. In the cases they cite of *Maxillaria* (see also Porsch, 1909; Dodson & Frymire, 1961b), the pollenlike cells appear to contain starch and serve as an actual nutritional reward for bees that collect them. Porsch (1909) cited a similar case in *Rondeletia* (Rubiaceae). Vogel (1978) later used the term pseudopollen for trichomes that mimic pollen and attract pollinators by deceit. Among groups that use pollen-mimicking trichomes in this way are members of the Commelinaceae (*Tradescantia* and *Commelinantia*) and orchids such as *Calopogon.* Following Vogel's usage no reward is, of course, obtained.

Nonfunctional, Dimorphic Pollen.—A number of species of angiosperms have dimorphic pollen associated with a dimorphism in pollen function. One form of the pollen serves as the male gametophyte, the other, sterile form, serves as a reward for pollinators. Vogel (1978) described several cases of plant species which have sterile pollen that is used as a mimic of pollen to lure potential pollinators into appropriately visiting the flowers. However, here we are concerned with a

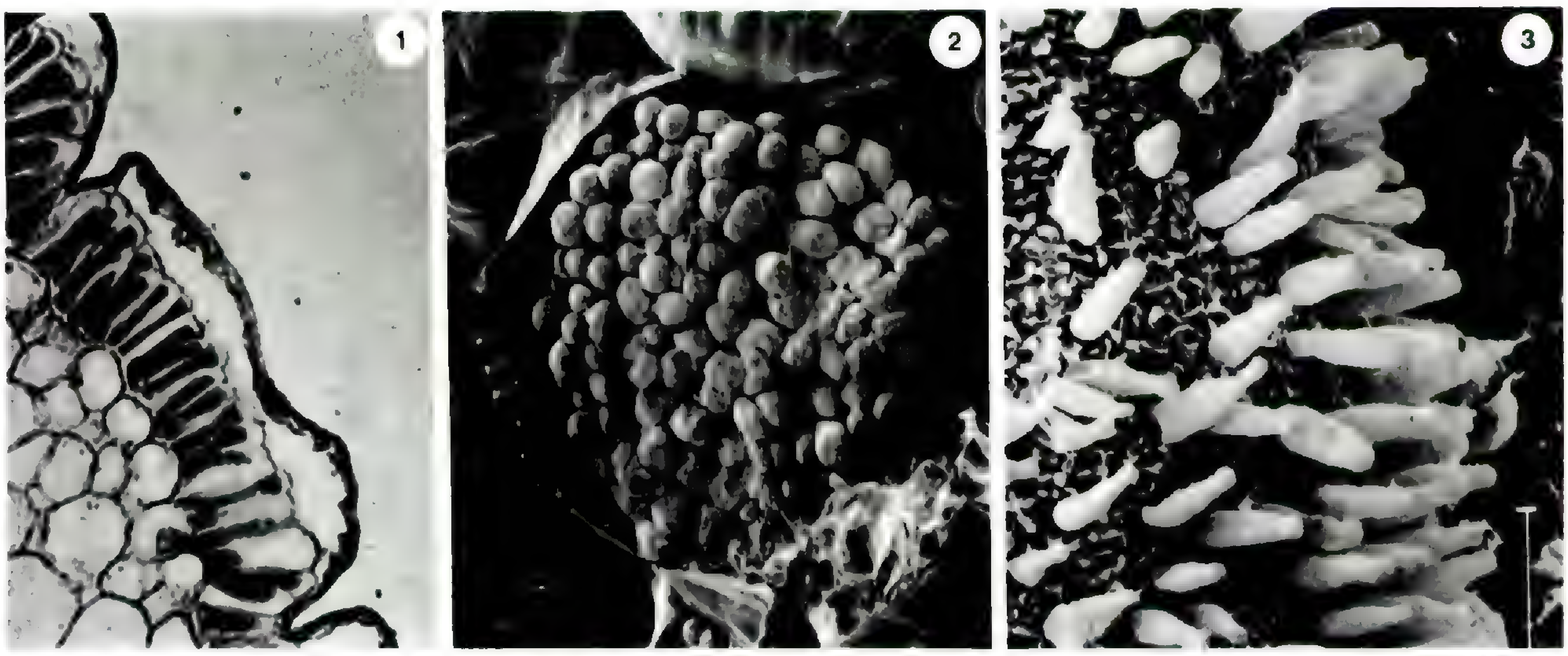
derivitive of functional pollen that serves as a reward in its own right. Classical cases of food pollen occur in *Cassia* (Leguminosae, Tischler, 1917) and *Melastoma* (Melatomataceae, Forbes, 1882). However, the extent of the phenomenon in these large genera is unknown, and it has not been investigated recently. We have been unable to verify the presence of dimorphic pollen in any of the species of *Cassia* we have examined.

More recent cases of dimorphic pollen have been reported in *Tripogandra* (Commelinaceae, Lee, 1961), *Tetracera* spp. (Dilleniaceae, Kubitzi & Baretta-Kuipers, 1969), and *Lecythis pisonis* and *Couropita guianensis* (Lecythidaceae, Mori et al., 1980). In *Tripogandra* there is only the supposition that the two pollen forms serve different functions, and in *Tetracera* the sterile pollen is found in perfect flowers of New World species that are labeled as being androdioecious, but which are functionally dioecious. The sterile pollen type could, therefore, be simply the remnant of the former, sexual flower, a form of deception, or an actual reward. Within the Lecythidaceae, there is ample documentation of large, pollinating bees feeding on the sterile form of the pollen while becoming dusted on the back with functional pollen.

Secretions Other than Sugar from Floral Nectaries.—The locations and types of floral nectaries have been thoroughly discussed by Fahn (1952) and Kartashova (1965). However, sugar-dominated secretions from structures other than typical floral nectaries can serve the same function. The lapping of stigmatic fluid from *Ephedra campylopoda* (Porsch, 1910), *Gnetum* (van der Pijl, 1953), and some palms (e.g., *Chamerops humilis*, personal observation) by insects has been linked with pollination. Copious, sweet stigmatic secretions of *Anthurium* (Araceae) that serve to attract pollinators have been reported and illustrated by Dauman (1930) and Croat (1980). All of these secretions are predominantly sugar solutions, but apparently can also contain amino acids as well (Baker, 1978). According to Martin (1969) and Fahn (1979), secretions of wet stigmas are usually composed primarily of oil and amino acids with small amounts of sugar. While it is apparent that more chemical analyses are needed, it is possible that there has been a selective modification of the composition of stigmatic secretions that are used as pollinator rewards.

Secretions from extrafloral structures that are parts of a compound inflorescence that functions as a flower (e.g., in the Araceae and the Euphorbiaceae) can also serve as "floral" rewards.

Oils.—The last nonpollen and nectar reward that we want to discuss is floral oil. This group of florally secreted chemicals was only recently recognized, but since its first report (Vogel, 1969) has been intensively studied by Vogel (1974) and our laboratory (Simpson et al., 1977, 1979; Seigler et al., 1978; Neff & Simpson, 1981). The term floral oils, it should be pointed out, is now used only for nonvolatile oils, not the essential oils that serve as odor attractants (although these may be mixed with floral oils), or as sexual attractants. It is becoming increasingly apparent that floral oils are one of the most widespread alternatives to pollen and nectar used as rewards for flower-visiting insects. We will, therefore, discuss floral oils in more detail than the other rewards mentioned above. In particular we will look at the taxonomic distribution of oil-secreting flowers, the structures of the organs that produce the oils, and the nature of the compounds



Figures 1–3. Types of elaiophores, or oil-secreting floral glands.—1. An epithelial elaiophore shown in cross-section, showing the highly differentiated layer of epidermal secretory cells covered by a common cuticle (×180).—2. A portion of an epithelial elaiophore of *Krameria grayi* (Krameriaceae) viewed under SEM (×181). See Fig. 4 for a view of an entire elaiophore.—3. Trichome elaiophores of *Trimezia* sp. (Iridaceae) from Goias, Brazil (×62).

produced. We will also elaborate upon the collection of the oils by specialized bees and indicate what is known about oil use.

It has been known for at least 200 years that various angiosperms such as the members of the Malpighiaceae and the genus *Krameria* have large glandular structures on the flowers. Before 1969, it was assumed that these structures were nectaries or remnants of functional nectaries. Vogel (1969) was the first to demonstrate in convincing detail that structures which he named elaiophores secreted lipids rather than nectar. In his later treatment (1974), he provided a detailed description of two kinds of oil-secreting organs, trichome and epithelial elaiophores, and listed five angiosperm families in which he thought they occurred. Trichome elaiophores (Fig. 3) are glandular trichomes that secrete lipids. They usually occur in patches on the corolla, but they can also occur on the stamens or ovary bases. The apical cell (or cells) of each trichome secretes oil that collects under the surrounding cuticle or in spaces between the trichomes. Vogel (1974) found evidence of these elaiophores in the Iridaceae, Orchidaceae, and Scrophulariaceae.

Epithelial elaiophores (Figs. 1, 2) are areas of glandular tissue with lipid-secreting epidermal cells. In this case the oils accumulate under the collective cuticle. Vogel (1974) listed three families, Orchidaceae, Malpighiaceae, and Krameriaceae, with taxa that appeared to have this type of elaiophore. On the basis of anatomical evidence, Vogel (1974) hypothesized that the oils were physically secreted from both types of elaiophores through pores in the cuticle. The oils seemed to be forced through the pores by female anthophorine bees equipped with a scraper of bristles on the front and/or mid legs or sopped up by pads of absorbant hairs on the forelegs. He diagrammed (1974: 468) what he believed to be the motions of the legs of *Centris* during the process of forcing oils through the pores of an epithelial elaiophore of *Stigmaphyllon* (Malpighiaceae).

In addition to his morphological studies of elaiophores, Vogel (1974) called attention to the fact that these oils are collected only by certain female bees of

the family Anthophoridae. Both the production of floral lipids and their collection appeared to be restricted to the New World although he indicated two genera of Scrophulariaceae (*Diascia* and *Bowkeria*) native to South Africa which may have flowers that secrete oils. Nothing is known of the pollinators of either genus. In several instances Vogel documented oil production with various chemical tests and personally observed oil collection by anthophorines in South America. In other cases, such as *Krameria,* he postulated oil production and its collection on the basis of floral anatomy and distributional records of bees.

Vogel ascertained for several genera that the secretory products were lipids by showing their lack of miscibility with water. His subsequent use of thin layer chromatography demonstrated that the secretions contained mixtures of several compounds. In most cases one or two of the components was present in greater quantities than the others. For *Calceolaria* he carried the analyses further and, in collaboration with Dr. F. Caesar (Vogel, 1974: 88–121), investigated the structures of the compounds involved. They concluded that the lipids of *Calceolaria pavonii* consisted primarily of diglycerides (which they called monoglycerides) with a β-hydroxy fatty acid and an acetate attached to each glycerol backbone. They also reported small amounts of free fatty acids in the mixtures.

Finally, Vogel hypothesized that the oils are used in place of nectar as the liquid component of the larval provisions of the solitary anthophorine bees. He examined the nests of several species, including fresh nests of *Tapinotaspis caerulea* and older, somewhat degraded, nests of a *Centris* and analyzed their contents. In addition to lipids he found traces of sugars that included fructose, sucrose, and di- and triglycerides. Only triglycerides are uncommon in plant nectars. Nevertheless, because the sugars were present in such small concentrations, Vogel (1974) concluded that the oils were a replacement for nectar in the larval food.

Since 1974, Vogel has reported three genera in two additional families, the Primulaceae and Cucurbitaceae (Vogel, 1976a, 1976b), which appear to have trichome elaiophores. In contrast to all of the groups reported before, one of these genera, *Lysimachia,* is almost entirely temperate in distribution. Both of the members of the Cucurbitaceae (*Momordica* and *Thladiantha*) are restricted to the Old World tropics. Moreover, entirely different groups of bees from those in the New World tropics, species of *Macropis* (Melittidae) and *Ctenoplectra* (Ctenoplectridae) reportedly collect the oils of these genera.

We have been investigating the phenomenon of floral oil secretion in the Krameriaceae and other New World groups for several years. In many cases our studies have confirmed Vogel's observations and conclusions. However, our data differ in some cases from his and we have been able to add to his observations. We have, for example, recently confirmed that the Solanaceae contains at least one genus, *Nierembergia,* that produces floral oils (Seigler, Simpson and Neff, in preparation). *Nierembergia gracilis* in Argentina is visited primarily by oil-collecting anthophorines (*Tapinotaspis* spp. and *Centris* spp.). Our chemical analyses of the extracts of the portions of the petals with secretory trichomes have shown that they produce, among other things, the same types of oils as other oil flowers.

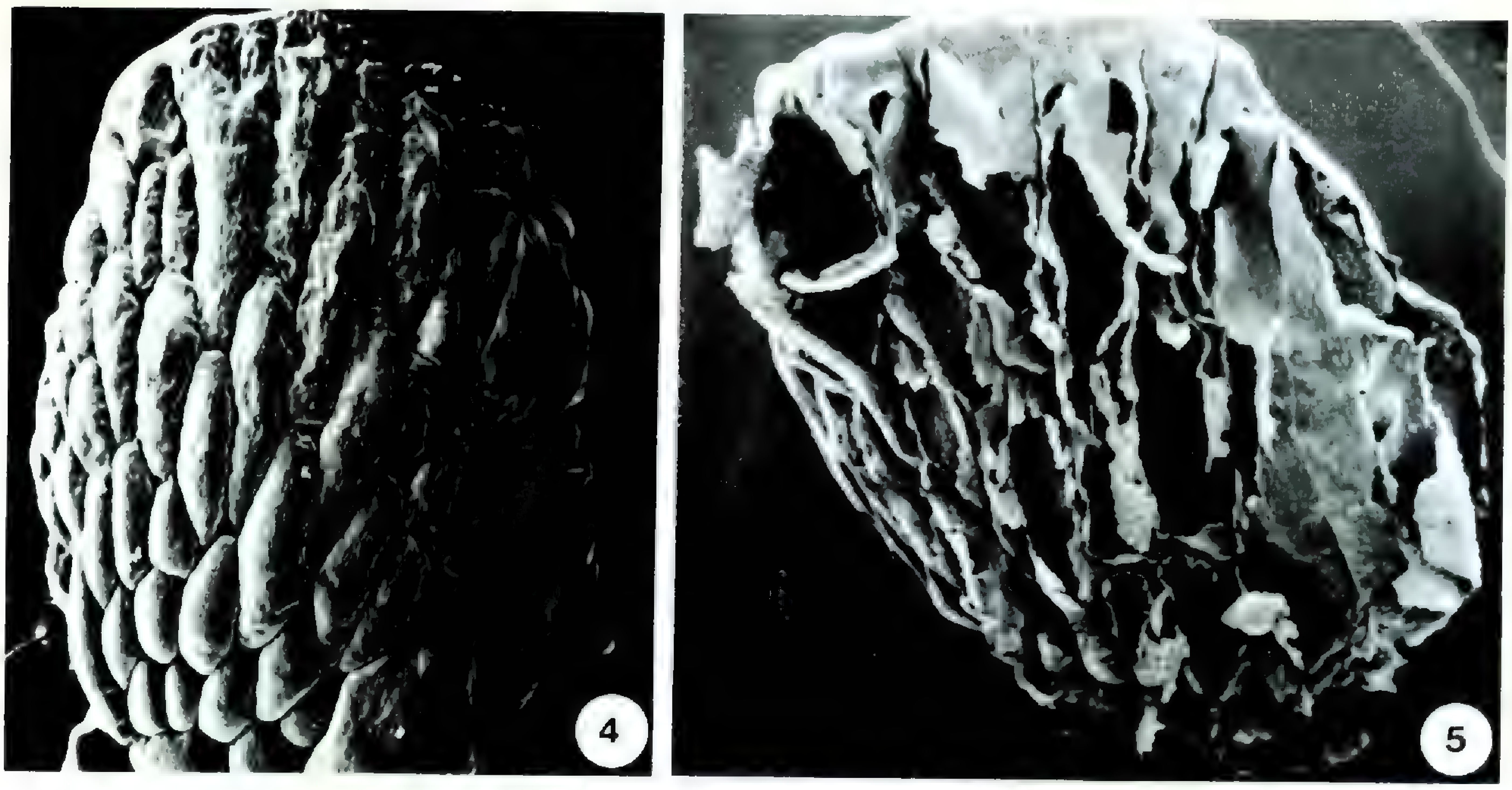
Most of our studies, however, have centered around *Krameria* and *Centris,*

its primary pollinator. *Krameria* is the sole genus in the Krameriaceae, a small group of about 15 species that has been variously aligned with the Leguminosae and the Polygalaceae. A synthesis of morphological and anatomical data suggests that a placement in the Polygalales is most realistic (Simpson & Skvarla, 1981). The flowers of all *Krameria* species are zygomorphic with five, separate, showy sepals. The five (or four) petals are reduced, two or three of them form a flag above the superior ovary and the remaining two have become lens-shaped glands flanking the ovary (Fig. 4). The glandular petals are 2–4 mm in diameter and can contain a milligram of oil per flower (not 0.9 mg per gland as reported in Simpson et al., 1977). In this case, therefore, entire petals have been modified into elaiophores.

We have examined in detail, by light and scanning electron microscopy, the structure of the elaiophores of the Krameriaceae (Figs. 1, 2, 4) and Malpighiaceae. In neither case did we find evidence of pores in the cuticle. Schnepf (1969) earlier found no pores in the cuticle of the trichome elaiophores of *Calceolaria*. Unvisited flowers, particularly those of the Krameriaceae, do not have free oils on the gland surface. Observations of glands after bee visitation clearly shows that during the collection process, female *Centris* rupture the cuticles (Fig. 5) while scraping the surface.

We have also examined the glands of *Krameria* using transmission electron microscopy (Simpson & Johnson, in preparation). The only previous work of the ultrastructure of oil-secreting glands was carried out by Schnepf (1969). He sectioned and described the multicellular apices of oil-secreting trichomes of *Calceolaria rugosa*. He pointed out the large quantities of endoplasmic reticulum (ER) in the dense cytoplasm and described what he termed complexes of endoplasmic reticulum and leucoplasts. Dictyosomes were especially noticeable in young secretory cells. The outer cell wall of the secretory cells was uneven, but generally thick compared to the walls of the nonsecreting stalk cells of the gland. He hypothesized that the oils were somehow able to penetrate through the thinner parts of the cell wall and collect under the cuticle. Despite his efforts, Schnepf (1969) was unable to locate large areas of oil accumulation within the cells or any apparent precursors of the oils.

Our studies showed many of the same features described by Schnepf. However, it should be pointed out that dense cytoplasm and relatively large amounts of ER are characteristic of plant secretory cells in general (Fahn, 1979). We have also noticed what appear to be leucoplasts in the cytoplasm and evidence, particularly in young cells, of vesicle formation by the ER. With the exception of normal lipid droplets, we have also been unable to pin-point areas of lipid accumulation within the cells. Fresh sections cut with a freeze microtome and stained immediately with Sudan black, a stain specific for lipids, showed a distribution of the stain throughout the cytoplasm. In older cells, there is a conspicuous shrinking of the cytoplasm from the outer cell walls producing a space between the plasmalemma and the cell wall. Schnepf found no such pulling away in the cells of *Calceolaria*. He did, however, find a similar structure in the secretory glands of *Salvia pratense* (Schnepf, 1972). The glands of *Salvia* are not oil glands and Schnepf postulated that the material which accumulated in the space between the plasmalemma was mucilage. We have stained fresh, freeze-



FIGURES 4–5. Epithelial elaiophores of *Krameria cuspidata* before (Fig. 4) and after (Fig. 5) visitation by an oil-collecting *Centris*. The cuticle under which the oils collect (Fig. 4) has been ruptured (Fig. 5) by the scraping movements of the fore and mid legs of the bees. Both ×20.

sectioned material with both ruthenium red (indicative of aqueous materials) and Sudan black. The space between the plasmalemma and the cell wall stained with neither. We must conclude therefore, that, unlike tissues of oil seeds that accumulate oil within the cells (e.g., *Sinapis*, Rest & Vaughn, 1972), oil-secreting cells transport the oils as soon as they are manufactured, or store very small quantities at a time uniformly throughout the cell. We know that oil secretion begins before the flowers open because unopened buds are forced open by bees who scrape the glands. Likewise, it appears that even after the cuticle is ruptured by an initial visit, the glands continue secreting, at least through the initial part of anthesis.

Our chemical analyses of the lipid secretions of *Krameria*, several Malpighiaceae, Iridaceae, and *Nierembergia* showed that the principal components of the oils differ from those reported by Vogel (1974) for *Calceolaria*. Vogel and his collaborator concluded that the majority of the oil they analyzed was in the form of a glyceride. While we found traces of glycerides in some samples (Seigler et al., 1978), we estimate that about 90% of the lipids is in the form of free fatty acids. Free fatty acids are relatively rare in plant tissues. Moreover, the fatty acids have an acetyl group in the β position, an unusual position for substitutions in fatty acids. We should mention, however, that the β-acetoxy fatty acids we have found (saturated acids with chain lengths of C16, C18, and C20), are the same as the fatty acids which Vogel found to be constituents of his glycerides. Analyses of epithelial elaiophore secretions of *Malpighia glabra* and *Mascagnia macroptera* (Malpighiaceae) and trichome elaiophore secretions of *Trimezia* sp. (Iridaceae) and *Nierembergia* all showed that they, like *Krameria*, contained β-acetoxy fatty acids. *Nierembergia*, however, contained a wider array of lipids and phenolics than the other species.

We also analyzed the oils of *Lysimachia ciliata* proposed by Vogel (1978) to

be an oil-producing species that is collected by female *Macropis*. Like the neotropical taxa visited by anthophorine bees, this species seems to contain free acetoxy fatty acids, but the extracts contain many other compounds as well. The principal components of the oils appear to be terpenes. It is, therefore, not clear that the system in *Lysimachia* is strictly comparable to that of the neotropical species visited by anthophorine bees. We are presently attempting to analyze other purported Old World species of oil flowers.

Buchmann (1978; Buchmann & Buchmann, 1981) recently reported that female anthophorine bees of the oil-collecting genus *Paratetrapedia* visit *Mouriri myrtilloides* (Melastomataceae) in Panama and he analyzed the secretions of glandular areas on the connectives of the anthers. His analyses demonstrated an array of classes of chemicals in the secretions, including fatty acids, amino acids, short chain acids, glycosides, and saponins. On the basis of the studies carried out by Buchmann, it is not possible to determine if *Mouriri* actually possesses the same syndrome of oil production as the other New World taxa Vogel (1974) and we have examined. The extracts he examined did contain numerous fatty acids, but he did not indicate if they were substituted or not. In addition, many of the components that he found in the oils of this species appear to be rather toxic (as food) to insects. His hypothesis (in press) that the bees which collect *Mouriri* oils may have to detoxify them suggests a use different from that of the oils of the other plants studied. Finally, Buchmann & Buchmann (1981) observed *Trigona* bees collecting *Mouriri* oils and placing them in the scopae separate from pollen. *Trigona* has never been reported collecting floral oils from any of the flowers previously investigated. Consequently, it appears that *Mouriri* and its relatives have a system of floral rewards different from that currently considered as floral oils.

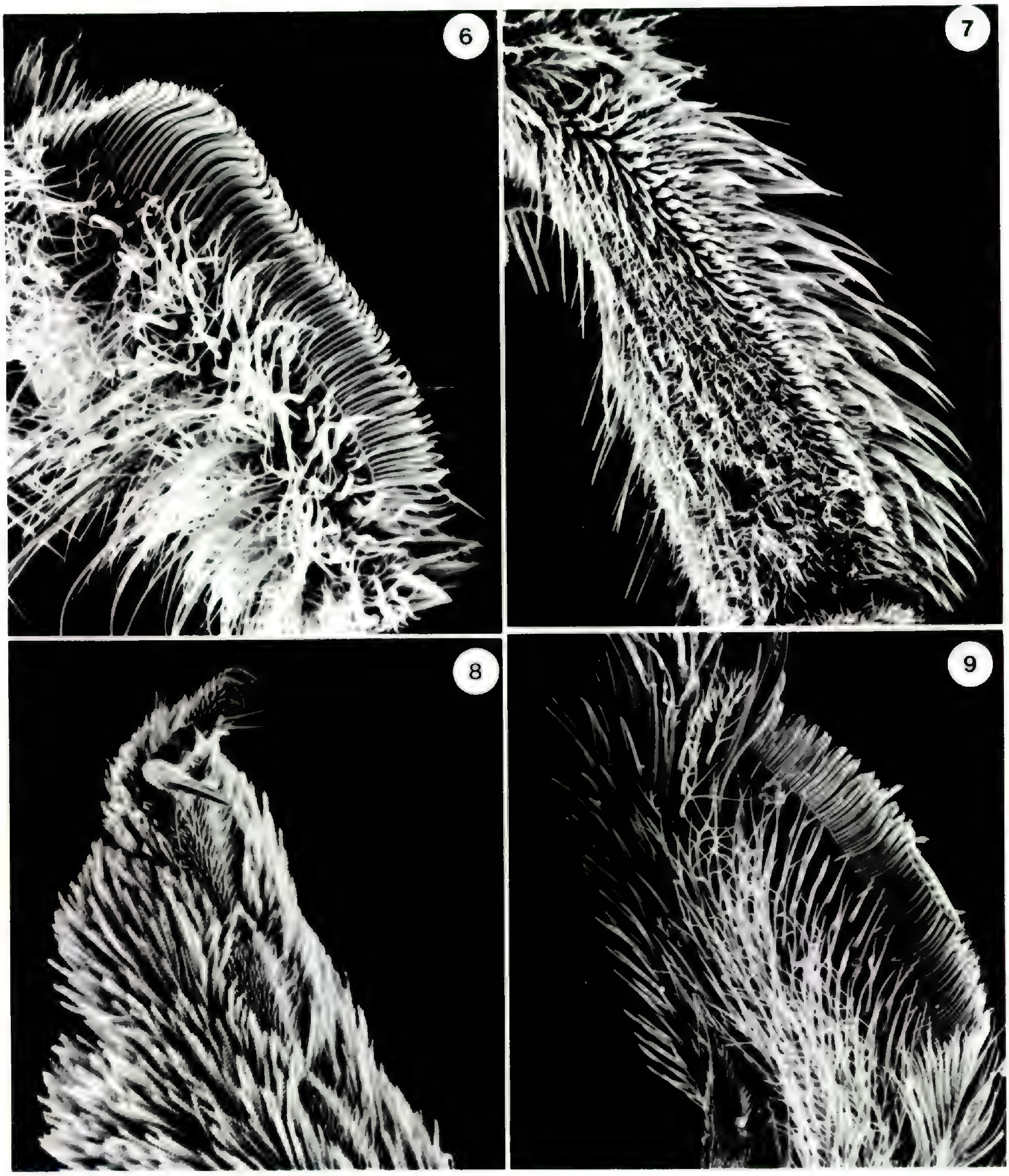
Because of conflicting reports, we also tried to determine if the glandular secretions of *Krameria* contained sugars. Analyses of nest contents of oil-collecting bees have shown that some contain appreciable amounts of glucose and fructose (Simpson and Neff, unpublished). It is known that adult oil-collecting bees visit plants other than their oil hosts for nectar, and it has consequently been tacitly assumed that any sugars in the larval provisions came from nonoil plants. If there are sugars in the elaiophore secretions, they may account for the sugars found in nest provisions. Percival (1961) and Baker (1978) have reported the presence of sugars in the "nectar" of several species of supposed oil flowers of the Malpighiaceae. Since Vogel (1974: 531) hypothesized that the elaiophores of the Malpighiaceae are derived from extrafloral nectaries, sugars might logically be expected to still be present in their secretions. However, if sugars are present in large quantities in the elaiophore secretions, Vogel's suggestion that the oils are used instead of nectar is unfounded. What is necessary to determine is the quantity of sugars in elaiophores if they are present. Small quantities of sugars are found in most plant secretions such as gums, latexes, etc. Likewise, lipids are commonly found in nectar (Baker & Baker, 1975), but their quantities are usually very small relative to the total solution.

We therefore analyzed simple gland extracts, material from squashes of entire glands, extracts of macerated glands, and extracts of macerated calyx lobes (of Malpighiaceous species from which the glands had been removed) of species including *Krameria lanceolata*, *Malpighia glabra*, and *Stigmaphyllon* sp. (ex-

amined by both Percival and Baker). Whenever extracts were made, over fifty glands or calyx lobes were used. The plant material was extracted with distilled water, and the decanted extracts evaporated to dryness. The residue which remained was taken up in a very small quantity of methanol and spotted on cellulose 300 N plates (Stahl, 1969: 814) and visualized with standard reagents. In no case have we been able to find any traces of sugars. Further study is obviously required, but clearly sugars are not significant components of the mature elaiophore secretions of the species we have examined.

When oil collection was first reported by Vogel (1969), and its presence in anthophorine nests confirmed (Vogel, 1974), it seemed assured that the primary role of the oils was to serve as a larval food source. The fact that nectar is now known to be present in significant quantities in some of these nests (Neff and Simpson, in press), raises some doubts about nutrition as the sole use of the oils. Floral oils should provide a concentrated energy source that could allow foragers to show a higher energy profit than bees foraging just for pollen or nectar. Available data on this point is sparse and inconclusive. Raw (1979) found that *Centris dirrhoda* foraging for oil and pollen on *Malpighia punicifolia* in Jamaica had very high floral visitation rates (41.8 flowers per minute) and was estimated to be able to complete a pollen-oil foraging run in seventeen minutes. In our studies, principally on *Krameria* species and several different species of the Malpighiaceae, we typically find much lower floral visitation rates (3.4–7.5 flowers per minute on *Krameria* and 5.0–19.2 on *Malpighia glabra*). We have also not observed foragers which collect pollen from their oil hosts. In addition, individual oil-foraging bouts are quite prolonged (occasionally over 30 minutes). As yet, it is thus impossible to formulate an energy budget for any oil-collecting bees, but we are planning to attempt this in the immediate future. Since floral oils may have qualities other than a high caloric value, we have proposed a number of alternative, but not mutually exclusive, possibilities for floral oil use. Alternative explanations we have proposed are: that the oils are incorporated into the nest linings, that the oils serve a fungicidal, bacterial or anti-predator function, or that the oils help to prevent water from being absorbed into the nest provisions (this last was suggested to us by Jerry Rozen). To date the only one of these we have been able to test is the possible fungicidal activity. We have tested (with the help of Robert Slocum) *Krameria* gland extracts against three species of fungi (*Aspergillus flavus, Saccharomyces cerevisiae,* and *Fusarium* sp.) known to be pathenogenic in solitary bee nests (Batra et al., 1973). The tests proved to be negative. Consequently, while many short chain fatty acids have a fungicidal activity (Wyss et al., 1945), those of *Krameria* appear to have no such effect. In fact, in the agar cultures on which we placed filter paper discs impregnated with *Krameria* oils, the fungi appeared to be fully capable of metabolizing them.

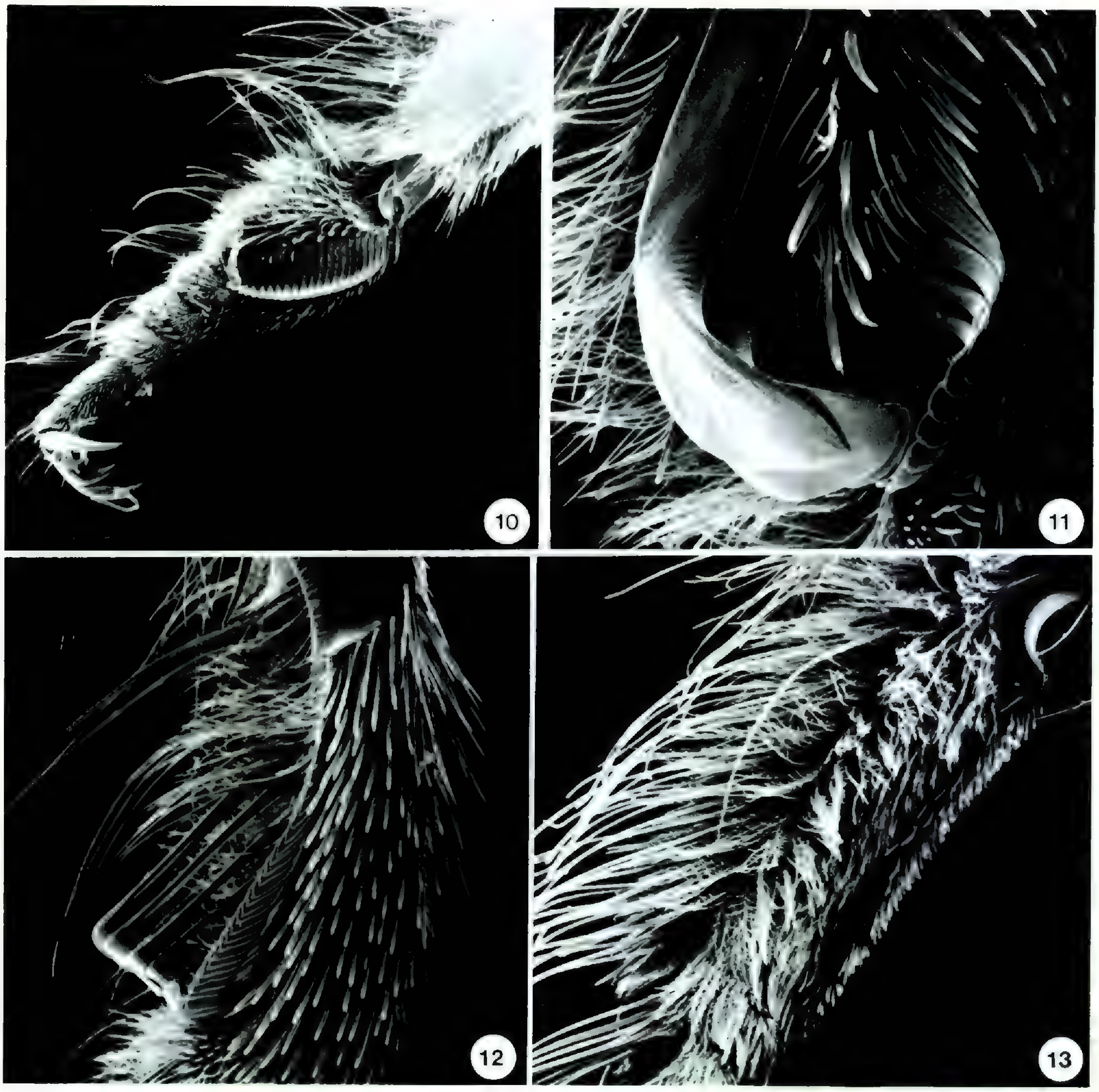
We have not yet been able to test the other hypotheses, but think that it is unlikely that the bees are incorporating the lipids into the nest lining because closely related anthophorines which do not collect oils construct virtually identical kinds of nests. Moreover, pollen is frequently incorporated into the scopal loads with the oils, yet pollen is not part of the nest linings of the taxa we have examined. At the present time therefore, it still appears most likely that the oils are used as one of the primary larval metabolites. The nutritional hypothesis gains support from the recent finding that the larvae of certain species of *Anthophora*



FIGURES 6–9. Oil-collecting structures of female anthophorine bees.—6. Right forebasitarsus of *Tetrapedia maura*, Tetrapediini (×79).—7. Right forebasitarsus of an undescribed *Tapinotaspis*, (*Tapinorhina*) Exomalopsini (×65).—8. Tarsus, left midleg (distal portion) of *Tapinotaspis* (*Tapinotaspis*) *chalybaea*, Exomalopsini (×43) showing the brushlike collecting hairs of this species.—9. Basitarsus, left foreleg of *Paratetrapedia maesta*, Exomalopsini (×83).

consume the maternally secreted fatty lining of their larval cells (Norden et al., 1980). *Anthophora* is a genus of nonoil collecting bees closely related to the oil-collecting anthophorines.

The oil-collecting structures of female Anthophorinae exhibit a wide array of morphologies ranging from long, sickle-shaped, relatively straight rows of simple setae to hoodlike cups of highly modified setae or pads of finely branched hairs



FIGURES 10–13. Forelegs of species of *Centris* species (Anthophorini, Centridini) showing the variations of the oil-collecting structures present in this genus.—10. Tibia and tarsus of a *Centris* aff. *tricolor* which collects on flowers with epithelial elaiophores (×24).—11. Left basitarsus of *C.* aff. *autrani* which collects oils from flowers with trichome elaiophores such as *Calceolaria* spp. (×121).—12. Left basitarsus of *C. versicolor,* a collector of oils from species of the Malpighiaceae, all of which have epithelial elaiophores (×62).—13. Left basitarsus of a nonoil-collecting *Centris, C. pallida* showing the loss of the oil-collecting structures (×62).

(Figs. 6–13 and Neff & Simpson, in press). As pointed out by Vogel (1974), there is a good correlation between the type of collecting structure and the type of elaiophore of the plants visited. Species of bees with only pads of hairs on the basitarsi visit only flowers with trichome elaiophores, presumably because they are incapable of scraping and rupturing the cuticles of epithelial elaiophores. On the other hand, species with scraping combs can, and do, visit plants with either type of elaiophores.

We have examined in detail the collecting structures of oil-collecting anthophorines (Neff & Simpson, 1981). These studies suggest that oil-collecting

may have arisen only once, or at most twice, in this family and that collection on plant species with trichome elaiophores preceded that of collection from epithelial elaiophores. Within *Centris* (Figs. 10–13), however, there is an ancestral association with epithelial elaiophores, particularly those of Malpighiaceae, independent losses of the ability to collect oils (with a corresponding reduction or loss of the collecting structures), and a variety of modifications of the oil-collecting apparatus related to the radiation in the spectrum of oil-producing hosts (Figs. 6–13).

We have studied in some detail the foraging behavior of marked females of *Centris atripes* in mapped populations of *Krameria lanceolata* in Austin, Texas. While oils are frequently incorporated into the scopal loads of pollen foraging bees, extensive observations indicate that oil foragers rarely carry significant amounts of pollen in their scopae. In this case at least, pollen foraging, which invariably involves plants other than *Krameria*, must occur after *Krameria* visitation. Oil foragers usually show extreme site constancy in our study area. One bee that was followed for 34.5 minutes, visited 119 consecutive *Krameria* flowers and buds within an area of 10 m^2. However, some individual foragers move on a regular basis between populations 50 to 100 m apart. The same marked female bees were observed day after day in the same populations of *Krameria* which are composed of what appear to be 10 to 25 flowering individuals. Controlled pollinations have shown that *Krameria lanceolata* is self-compatible but not autogamous. Within a plant, therefore, geitonogamy appears to be unavoidable as individual bees usually visit a high proportion of the open flowers on any particular plant. However, individual bees may frequently approach, but rarely revisit, flowers they have recently visited on a given plant.

We have performed a series of preliminary experiments to help to understand what are the specific attractants of *Krameria* flowers and how female *Centris* are able to recognize flowers they have recently visited. The experiments have involved removal of various floral parts as well as exposure of gland secretions on filter paper discs to foraging bees. Observations of the antennae dipping activities of female *Centris* indicates that the primary short-range cues are olfactory, although the isolated gland secretions on filter paper never attract female bees. Scent production, at least to a human nose, seems to be localized in the elaiophores in *K. lanceolata* and *K. grayi*, yet, typical oil gathering motions of female *Centris* were still observed when either the elaiophores or the stamens were removed from flowers. In the former case the bees simply went through the scraping motions with the legs grazing only the sides of the ovary. Current evidence suggests that a hierarchy of cues is involved which includes floral form and color, an odor (volatile oils) mixed with the fatty oils, and scent marking, either passive or active, by the bees themselves. Further experiments are planned to unravel the sequential effects of these factors.

In the Austin area *Krameria lanceolata* is the only native oil plant. To study the relative constancy of female *Centris* when presented with two potential oil hosts, we placed potted, blooming plants of *Malpighia glabra* in a patch of *K. lanceolata*. *Malpighia glabra* (Barbados cherry, or acerola berry), is not native in central Texas, but it is planted in Austin as an ornamental. *Centris atripes*, our primary study bee, is quite widespread in the southwestern United States and throughout Mexico and does occur naturally in areas where *Malpighia glabra* is

native. We assume, however, that the bees with which we were working were naive to *Malpighia* since we have found none planted near the research station. After a few minutes exposure to the potted plants, the *Centris* foragers switched from *Krameria* to *Malpighia* and proceeded to scrape repeatedly all the open *Malpighia* flowers. After this initial active bout of foraging, the bees began to move back and forth between *Krameria* and *Malpighia*. These preliminary experiments suggest that these bees lack a strong innate preference for a particular oil host, at least among flowers of similar size and color. It is therefore possible that, as in many other pollination systems, constancy in foraging may be mediated by levels of resource availability.

Knowledge of the blooming patterns of oil plants in a community should be particularly enlightening in view of the fact that *Centris* and its relatives are major pollinators of many tropical species (Frankie et al., 1976). Our own work in the arid scrub vegetation in northwestern Argentina indicates that a single oil-collecting species, *Centris brethesi*, is one of the dominant pollinators of the entire community, and its interactions with various pollen, nectar, and oil hosts have led to fairly complicated phenological patterns. These kinds of interactions should be even more interesting in more mesic tropical environments where both the diversity of oil collecting bees and oil flowers increase markedly. We therefore plan to pursue studies of oil plants as a requisite component of the pollination of tropical communities.

Conclusions

While pollen and nectar are without doubt the primary floral rewards, selection has promoted the use of numerous alternative rewards in an impressive number of plant species. We conclude, as have others, that selection favored the elaboration or use of these rewards because plants which possessed them were able to capture a segment of the pollinator community not used by other plants in a community and/or achieve greater constancy of visitation.

If the use of alternative rewards insures greater constancy and, presumably, more effective pollination, we might ask why more plants have not turned to them. We believe the answer is two-fold. First, many alternative rewards are more expensive (energetically) than pollen and nectar, and, second, the use of an alternative reward often locks both the plant and the pollinator into a one-to-one relationship. While in the short run such specificity might be advantageous, it provides a situation conducive to relatively rapid extinction. It is likely that in such systems as those involving orchids and euglossines or figs and fig wasps, that coevolutionary radiation can occur rapidly, but that extinction also eliminates many species pairs.

For oil plants the situation is somewhat more complex since oil species have now radiated and oil-collecting bees do not appear to be species specific in their choice of oil hosts. If several oil plants co-occur within a community, they now appear to partition their pollinator fauna along the lines often observed for plants offering traditional rewards, namely, by temporal, spatial, or size displacements. Oil flowers also often have more options than some other plants which offer alternative rewards because their pollen can be, and is occasionally, used as a reward by oil-collecting bees. Consequently, they are not locked into a system involving a single, specialized reward.

If we ask why bees have turned to the collection of oils, the answer is not straightforward and final resolution of the question must await the accumulation of more data on the life histories of oil-collecting bees. If, however, larval nutrition is the primary use of the collected oils, it appears likely that their high energy content per unit weight relative to carbohydrates makes its use profitable. The discovery that non-oil-collecting anthophorine bees secrete maternally synthesized fatty oils from the Dufour's glands which are subsequently fed upon by the larvae provides support to the idea that fats are a superior food. On the basis of present reports, few groups of flower-visiting bees appear to be capable of metabolizing high lipid diets. More work is needed to assess the utilization of lipids by other groups of bees and to determine the degree of dependency of oil-collecting anthophorines on floral oils.

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GEOGRAPHICAL ASPECTS OF BIRD-FLOWER COEVOLUTION, WITH PARTICULAR REFERENCE TO CENTRAL AMERICA[1]

F. Gary Stiles[2]

Abstract

The overall objective is to compare the ecological impact of bird-flower coevolution in different geographical areas. However, it is first necessary to define the parameters of such coevolution in broader terms than those of the traditional "syndrome of ornithophily," which focuses very narrowly on some aspects of floral morphology. I recognize three distinct components of flower function: attraction, reward, and filtering mechanisms, and discuss their functioning in an ecological context, and as they relate to the genetic system or "pollination unit" of the plant. Then I turn to nectar-feeding birds, and discuss not only morphological, but ecological and behavioral specializations to flowers as a food source. These discussions develop explicitly my criteria for detecting and evaluating bird-flower coevolution. The different groups of birds known to feed regularly (as opposed to opportunistically) on nectar are then compared according to these criteria, to determine their relative degrees of specialization for, and dependence upon, a high-nectar diet. Different groups are found to vary widely in their degrees of specialization for flower-feeding, and it is evident that bird-flower coevolution has followed very different courses, and led to widely divergent ecological systems in different geographical areas. By any criteria the hummingbirds are the most specialized avian nectarivores, although they are approached in this regard by some members of certain passerine groups, notably among the sunbirds. Several groups of passerine nectarivores also occur with the hummingbirds in many New World areas; these groups show low to moderate degrees of specialization for nectarivory, either as pollinators or as parasites on the hummingbird-flower system. The New World tropics thus present a wide range of specializations for flower-feeding in their avifauna, and represent a particularly interesting area for study. Patterns of ornithophily and nectarivory are thus examined in detail for this area, concentrating specifically on Southern Central America, especially Costa Rica. The altitudinal and geographical distributions of the two main groups of hummingbirds, the hermits and nonhermits, are found to differ, as are the taxonomic and ecological affinities of their primary foodplants. The hermits are most numerous in wet lowlands and the adjacent foothills, and are primarily associated with large monocotyledonous herbs, notably *Heliconia*. The nonhermits reach their greatest taxonomic and ecological diversity in the lower middle elevations, and are the only group present at high elevations; they seem to have coevolved with the flowers of a variety of dicot families, and the bromeliads among the monocots. Passerine nectarivores occur primarily as parasites on the hummingbird-flower system (Coerebidae) and are important as pollinators only in seasonally dry areas when the hummingbirds are poorly represented.

Within the last ten to fifteen years the study of pollination has passed from a purely botanical pursuit to an extremely active field of ecology. This is especially true with respect to bird pollination systems: a resurgence of interest in the foraging ecology, energetics, and social behavior of nectarivorous birds is leading to a new and broader appreciation of their role as pollinators. This, in turn, is one of the major catalysts in the continuing emergence of a more balanced and

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[1] My ideas on pollination biology have been sharpened by discussion with many people, including OTS faculty and students, too numerous to mention here. However, I acknowledge a particular debt in this regard to H. G. Baker, G. W. Frankie, B. Heinrich, P. A. Opler, S. Salas, and L. L. Wolf. My studies in Costa Rica and a recent trip to Venezuela have been financed by the Vicerectoría de Investigacíon, Universidad de Costa Rica; by CONICIT; and, earlier, by the American Museum of Natural History. P. H. Raven provided several helpful suggestions and references for the manuscript, for which F. L. G. Sanders supplied criticism. Finally, I thank Missouri Botanical Garden and Gerrit Davidse for the opportunity to participate in this symposium.

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profound view of plant-pollinator coevolution. This new outlook is still evolving rapidly, and rather than attempt a theoretical synthesis, I will apply some of these new points of view to a geographical survey of bird-flower coevolution.

My specific objective is to compare the kinds and degrees of coadaptations between birds and flowers in different geographical areas, hoping thereby to arrive at a better understanding of the ecological and evolutionary impact of these coadaptations in different biota. By coadaptation, I am referring to the degree of ecological interdependence of bird and flower, as well as to the degree of morphological correspondence (as embodied by the well-known "syndrome of ornithophily"). The most highly coevolved system, then, is one in which the flower is completely dependent on the bird for pollination, and the bird requires the energy provided by the flower for breeding and molt: reproduction and perhaps even survival of either would be impossible without the other. Such coadaptation makes the species involved peculiarly vulnerable—what affects one will perforce affect the other—but it also makes possible the occupation of new ecological niches or adaptive zones (e.g., winter breeding in *Ribes speciosum* and *Calypte anna*, cf. Stiles, 1973).

In this paper I shall first review the kinds of coadaptations that can occur between birds and flowers, considering behavioral, physiological, and ecological as well as morphological parameters. I shall thereby develop criteria by which to compare the bird-flower coadaptations of different continents. I shall then discuss in more detail bird-flower coadaptations of the New World tropics, particularly Central America. Hopefully this analysis will lead to a deeper understanding of the ecological impact of these systems, and of the evolution of the groups of birds and flowers involved.

The Syndrome of Ornithophily Revisited

Until recently most studies of bird-flower coadaptations were devoted to demonstrating the existence of pollination by birds, and to elucidating the floral mechanisms involved. These adaptations are summarized in the well-known "syndrome of ornithophily" which represents the culmination of many years of observation and controversy (Faegri and van der Pijl, 1966), as well as a convenient starting point for the present discussion. Two things are immediately obvious from this "syndrome": the emphasis is narrowly focused upon the flower itself, ignoring many other aspects of the plant's biology that might affect bird visitation and pollination. Also, virtually nothing is said about possible specializations of birds for flower visitation.

In this paper I shall attempt to take a broader and less one-sided view of bird-flower coevolution. Elsewhere (Stiles, 1978b) I have discussed in some detail the various ways in which parameters of plant populations, and of the plant itself, can impinge upon pollination biology, with particular reference to bird pollination. For other discussions of this general theme, see Gadgil & Solbrig, 1972; Stiles, 1975; Wilbur, 1976; Pitelka, 1977; Bawa & Opler, 1977. Here I wish to emphasize aspects of floral biology *per se*, but without ignoring this broader context.

First, some definitions may be in order. Faegri & van der Pijl (1966) distinguish between "attraction unit" (those features that attract a pollinator from some distance away to the flower or inflorescence), and the "pollination unit" (within

which pollination occurs). In reality two distinct phenomena are being confused by these authors' use of "attraction unit": the attraction of the pollinators' *attention* to the flower, and the provision of a real or simulated reward that actually induces the animal to visit the flower. I restrict the term "attraction unit" (or component) to those mechanisms subserving the former function, and use "reward unit" (or component) for those accomplishing the latter. Clearly the functioning of the attraction component must be intimately related to the sensory biology of the flower visitors, while the reward component must correspond to some nutritional, sexual, or other need of the pollinator. Although this distinction may be blurred in some flowers (see e.g., Simpson, this symposium), it is clear enough in bird flowers: bright colors form the basis of the attraction component; nectar, of the reward component. Another function that I choose to distinguish is the restriction of access to the reward to a narrow segment of the potential spectrum of visitors attracted. The term "exclusion mechanisms" has been used here, but I prefer the term "filtering component" (or mechanism). At least in bird flowers, such limitations of the visitor spectrum are often not absolute exclusions but relative ones, based upon pollinator energetics: a flower not worth exploiting to some pollinators under some conditions may become profitable under others (e.g., Heinrich, 1975; Wolf et al., 1975, 1976).

Finally, the term "pollination unit" can be made more explicit by relating it to the breeding system of the plant (cf. Bawa, 1974; Cruden, 1977) and genetic structure of the plant population (e.g., Price & Waser, 1978). The "optimum pollination unit" might be defined as the minimum spatial separation of flowers over which movement of a given amount of pollen will produce maximum seed set (including seed viability, cf. Levin, this symposium). The "minimum pollination unit" would be the minimum separation of flowers (in terms of being on the same inflorescence, plant, or clone as well as physical distance) required for pollination to occur at all (see Stiles, 1978b). Only for obligately self-fertilizing flowers would the two terms be synonymous (the unit would be one flower in either case).

ATTRACTION

In ornithophilous flowers attraction is primarily, perhaps exclusively by color, though odor cannot be ruled out entirely in some cases (Stiles, 1976). The chief requisite for attraction is thus conspicuousness to birds, which will reflect the properties of avian vision and habitat features. Birds have their greatest spectral sensitivity and finest hue discrimination towards the long wavelength end of the visual spectrum (reviews in Sillman, 1974; Stiles, 1976), although the complex interplay of cone pigments and colored oil droplets makes the situation a great deal more complex than in mammals (e.g., Bowmaker, 1977). Moreover, hummingbirds at least may be able to perceive ultraviolet "colors" (Goldsmith, 1980); the role of this ability in foraging remains to be studied. The prevalence of ultraviolet patterns and nectar guides in relatively nectar-poor entomophilous flowers may make it possible for hummingbirds to avoid these flowers on sight. Certainly the vast majority of bird-pollinated flowers feature long wavelength colors in the attraction unit. The occurrence of other colors, or of contrasting colors, may add to conspicuousness against particular backgrounds (see Stiles, 1976). Another

factor may be the colors of the birds themselves: various authors have noted correspondences between the display colors of certain (mostly Old World) nectarivorous birds and some of their preferred flowers (Faegri & van der Pijl, 1966). Most often the colorful birds are males, who may show a hormone-mediated higher responsiveness to these colors (Ducker, 1970; Morton, 1979).

The manner in which the colors are displayed is related to a number of factors. The flower may carry the attractive colors if it is long-lived and/or in an open habitat. In many ornithophilous species immature flowers or bracts are also colorful, adding to the size and longevity of the visual signal. In other species, the need for a conspicuous, long-lived signal has been solved by the evolution of a large, colorful inflorescence (e.g., *Heliconia, Costus*, many bromeliads). The flowers in such cases are often ephemeral and inconspicuous except insofar as they contrast with the inflorescence, probably adaptations to help protect them from destructive nectar thieves (cf. Stiles, 1975, 1976). A variation on this theme is the incorporation of red or red-spotted leaves into the attraction unit (Jones & Rich, 1972; Stiles, 1978b).

REWARDS

Nectar is the only floral reward regularly offered to birds. Only one questionable case of regular pollen-eating has been reported for hummingbirds (Carpenter, 1976a), although it is common in parrots of the subfamily Loriinae (Churchill & Christensen, 1970; Forshaw, 1973). However, the flowers involved are often eaten by the parrots, whose role as pollinators—and hence participants in coevolutionary relationships with plants—remains to be studied in detail (cf. Paton & Ford, 1977; Ford et al., 1979).

Compared with insect-pollinated flowers, bird-pollinated flowers usually show higher nectar volumes, slightly to markedly lower concentrations, and considerably higher sugar production overall (Baker, 1975; Heinrich, 1975; Stiles, 1975, 1978b; Opler, 1981; Cruden et al., 1981). This reflects the high energy requirements of the birds, and both laboratory and field studies suggest that energetic criteria are the most important determinants of flower choice in nectarivorous birds (Hainsworth & Wolf, 1976; Stiles, 1976). The three dominant sugars in nectar, sucrose, glucose, and fructose are energetically equivalent, but sucrose usually predominates in nectars of hummingbird flowers (Stiles, 1976; Baker & Baker, 1981). Old World bird-flowers generally have nectars low in sucrose; their passerine pollinators may have difficulty digesting this sugar since experiments with European Starlings (a member of a family containing a number of facultative nectarivores) demonstrate that they cannot maintain weight on a high-sucrose diet (Schuler, 1977). Hummingbirds usually prefer sucrose-rich nectars in the field and under appropriate laboratory conditions (Stiles, 1976), but will use Old World bird-flowers freely in gardens, doubtless because of their high nectar volumes (Stiles, 1973, 1976).

Other components of nectar include amino acids, lipids, and polysaccharides (Baker & Baker, 1975). Probably none of these is nutritionally essential to nectar-feeding birds, which have access to such substances in insects and fruit, unlike most insect pollinators (cf. Baker & Baker, 1975; Gilbert, 1975; Ford & Paton,

TABLE 1. Rates of nectar extraction and feeding preferences among hummingbirds visiting two species of *Heliconia* in a Costa Rican second-growth area.[a]

	Heliconia Species			
	Heliconia latispatha		*Heliconia imbricata*	
Hummingbird Species	Slope of Extraction Line[b]	# Visits[c]	Slope of Extraction Line	# Visits
Amazilia tzactl	0.097	182	0.176	119
Thalurania furcata	0.125	70	0.119	201
Chalybura urochrysia	0.252	36	0.112	149
Phaethornis superciliosus	0.322	13	0.252	88

[a] Observations made June–Aug. 1971, 1972, 1974 in an area ca. 3 ha in size, of old second growth; *H. imbricata* was about 1½ times as abundant (in terms of numbers of flowers) as *H. latispatha* overall.

[b] Slope of the line of time spent probing flowers (y axis) vs. nectar extracted (x axis): the lower the slope, the more nectar can be extracted in a given time. Based on 35 or more observations except *C. urochrysia-H. latispatha* (N = 21) and *P. superciliosus-H. latispatha* (N = 13).

[c] Number of times a bird of a given species was seen visiting flowers of a given plant species during census walks through the study area. Each species shows a highly significant preference ($P < 0.01$ by chi-square test) for the flower at which it can most quickly extract nectar.

1976a). At low concentrations amino acids are not detected by hummingbirds; at high concentrations, they are rejected (Hainsworth & Wolf, 1976). This should place a selective premium on reducing amino acid concentrations in nectar, and Baker & Baker (1975) have indeed found that tropical bird-flowers have nectars with very low amino acid content. The more recently evolved North American hummingbird flowers have higher amino acid concentrations in their nectars—but still markedly lower than those of the presumably ancestral bee-pollinated species (Grant & Grant, 1968; Baker & Baker, 1975).

FILTERING MECHANISMS

I will discuss two sorts of mechanisms here: those tending to restrict visitation by nonpollinating animals, especially destructive ones; and those that enhance specificity of flower choice among potential bird pollinators.

Insect visitation may be reduced in bird flowers by a variety of mechanisms: red color (in addition to its conspicuousness to birds, this color is relatively inconspicuous to some bees, although probably not to many butterflies (Raven, 1972), dilute nectar (Baker, 1975; Bolten & Feinsinger, 1977), appropriate timing of nectar production (Stiles, 1975), and perhaps nectar composition. If taste conditioning occurs in insects as well as hummingbirds, the production of high-sucrose nectar may in itself favor hummingbird visitation (cf. Stiles, 1976). The hard floral parts and large nectar-sexual sphere distance mentioned in Table 1 more likely evolved as protection against destructive nectar thieves than against the "hard beaks" of pollinating birds. Opler (1981) demonstrated a direct correlation between nectar flow and flower weight among a large number of tropical plant species: the increase in weight coming largely from harder and thicker protective tissues in the perianth, as well as a longer corolla tube. In humming-

birds and presumably sunbirds the birds do not thrust the bill any further into the flower than necessary to enable the extensible tongue to reach the nectar; the tongue grooves fill with nectar most effectively in a confined space if the tongue is extended beyond the bill tip (Hainsworth, 1973; Schlamowitz et al., 1976).

Restricting visitation to a few of the potential pollinators can promote efficiency of pollination by reducing the frequency of mixed pollen loads. Specificity of flower choice, or "flower constancy," is important at the level of the individual pollinator; degree of specificity probably reflects the relative energetic profitabilities of the flowers available to each forager (Heinrich, 1976). Amount of nectar available, efficiency of nectar extraction, and cost of transport between flowers are probably the most important factors determining profitability at this level (Wolf et al., 1975). Different lengths and/or curvatures of corolla tubes can affect the extraction efficiencies of different hummingbird species in relation to differences (often subtle) in bill morphology; this in turn may strongly influence flower choice by the birds (for an example involving *Heliconia*, see Table 1: in each case the bird strongly prefers the species of *Heliconia* from which it can most efficiently extract nectar). Tubular flowers have the further effect of forcing the bird to orient its bill in a particular way when probing the flower, especially when bill and corolla are curved; this in turn facilitates placing pollen on a specific part of the bird, which can reduce mixing of pollen loads even on a relatively nonspecific pollinator (clearly an advantage for a rare plant species). This can open the way for a variety of highly specific morphological coadaptations (cf. Stiles, 1975; Brown & Kodric-Brown, 1979).

Bird flowers mostly fall into two broad morphological groups: tube and brush. Tubular flowers are in many respects the most highly evolved and the most likely to enter into specific coevolutionary relationships. Brush flowers generally house the nectar in a cup or short tube, out from which a "brush" of stamens extends. Visitors seeking nectar (or pollen) are liberally dusted with pollen, which is brought more or less haphazardly in contact with the stigmas. Many bee- and bat-pollinated flowers are of similar construction, and it may be that brush flowers simply represent a generalized adaptation to pollinators large in relation to flower size. As such they would be very ineffective filters—any visitor in a given size range could pollinate the flower. Brush flowers may, in effect, be specialized for pollination by a wide spectrum of taxonomically diverse visitors. For instance, the red stamens of *Calliandra* spp. (Mimosaceae) may represent an adaptation for drawing birds into an essentially chiropterophilous syndrome. Many regular pollinators of brush flowers are quite unspecialized in their flower visitation, such that pollination occurs more or less haphazardly as the animal blunders about in or on the flower. Such "mess and soil" pollination (Faegri & van der Pijl, 1966) may be carried out by bats, nonflying mammals (Carpenter, 1976a; Sussman & Raven, 1978), and birds such as lories. Nectar in brush flowers is available to any visitor that does not mind getting dusted with pollen; the potential for exclusive coevolutionary relationships is low.

Pollinator specificity can be enhanced if interspecific competition occurs between potential pollinators. Aggressive behavior and/or territoriality of dominant individuals or species can result in partial or complete exclusion of subordinate individuals and/or species from flowers that they might otherwise visit (Lyon,

1976; Wolf et al., 1976). The wide range in nectar production among sympatric hummingbird flowers may function in part as a resource gradient along which different hummingbirds might specialize according to their dominance status and energy needs (Feinsinger & Colwell, 1978; Stiles, 1978b).

POLLINATION UNITS

The production of relatively large amounts of nectar and protective tissue makes bird pollination quite expensive on a per-flower basis. Thus bird pollination will probably evolve only where the advantages, in terms of enhanced pollination, outweigh these expenses (see review in Stiles, 1978b). The pollination strategy of an ornithophilous plant amounts to making enough nectar available to attract avian visitors, while adjusting their movements between flowers to the size of the optimal (or minimal) pollination unit. This entails adjusting nectar availability in terms of the proportion of the pollinator's energy requirements that can be satisfied by a single flower, shoot, or clone, and thus determining the degree of interplant movement (Heinrich & Raven, 1972).

Bearing in mind that they but represent the ends of a continuum, we can distinguish two extreme foraging tactics of nectarivorous birds: route foraging or traplining, and territoriality (Feinsinger, 1976; Stiles & Wolf, 1979). The former is ideal for promoting cross-pollination, but if the plants are widely scattered many flowers may be missed. Territoriality restricts pollen flow to and from the defended area, but its effect on cross-pollination depends on the effectiveness of the defense, and on whether the territory itself contains one or many plants (Linhart, 1973; Ray et al., 1981). Within the territory, systematic foraging of the resident may maximize the proportion of flowers visited (Gill & Wolf, 1975; Stiles, 1978b). Whether territorial or traplining pollinators are favored will depend ultimately upon the plant's spatial dispersion and breeding system, and various parameters of morphology and phenology can be varied to favor one or the other type of pollinator, as has occurred in *Heliconia* (Stiles, 1975, 1979).

AVIAN ADAPTATIONS FOR FLOWER-FEEDING

I now wish to treat the various possible avian specializations for visiting and (at least in some cases) pollinating flowers. Although virtually all of these adaptations have been discussed previously, I know of no recent attempt to bring them together to present, in effect, a coherent "syndrome of anthophily" of the birds. This would seem to be a necessary first step in assessing the degree of specialization for flower visiting of any given species or group; this in turn could provide an indication of the overall evolutionary development of bird-flower coadaptations in any given region. The features listed in my "syndrome of anthophily" (Table 2) stress relative degree of specialization; a bird may be considered more or less specialized for flower visiting according to the extent to which it shows any particular array of features to a greater or lesser extent than do its nonanthophilous closest relatives or putative ancestors (where known). This procedure may somewhat deemphasize absolute degree of specialization in those cases where a group is in some way preadapted for flower visiting. For instance, small size may be viewed as a specialization for flower visitation (see below). The

TABLE 2. Specialization for flower-feeding in birds: the "syndrome of anthophily."

Characteristics of Birds	Characteristics of Flowers
1. Small body size; usually less than 20 grams	1. Most flowers small, nectar content usually 200 μl or less
2. Bill usually slender, often long and/or curved, matching flower corollas; occasionally hooked, awl-pointed, etc.; nasal operculum well developed	2. Nectar deep-seated, often at end of long and/or curved tube; hard flower parts (to be surpassed by nectar-robbers)
3. Tongue tip grooved, fringed, and/or capable of rolling into tube to take up nectar by capillarity, tongue extensible beyond bill tip; papillate tip for pollen feeders	3. Nectar relatively dilute, low viscosity, often in deep-seated chamber with narrow entrance
4. Gut with extensible crop for storage and rapid absorption of nectar, esophagus and intestinal openings close together, leaving stomach as a diverticulum into which insects pass, but little nectar (not necessary for pollen feeders)	4. Nectar with low amino acid content, main protein source insects.
5. Agility to reach flowers, especially hovering flight, sometimes large or strong feet to cling to inflorescence	5. Flower hangs free or faces outward or down to discourage insects
6. Aggressive behavior and often feeding territoriality well developed whenever flowers sufficiently abundant	6. Flowers stationary, visible, highly defensible resource
7. Excellent spatial memory; can recall location of flowers last visited in a dense array, or of flower clumps over wide areas and for long time periods	7. Flowers stationary, seasonal, patchy in distribution
8. Wide-ranging; seasonal movements on basis of flower abundance shifts	8. Spatial and temporal variations in blooming
9. Breeding and/or molt closely tied to flower abundance; nectar a necessary source of energy to meet expenses	9. Regularly recurring peak(s) of flowering each year, permitting birds to schedule their peak energy demands accordingly

Tennessee Warbler (*Vermivora peregrina*), a frequent flower visitor, is sufficiently small to be considered moderately specialized in this respect (8–9 g). However, its closest relatives in the genus *Vermivora* weigh scarcely more (8–11 g) but, like most of the family Parulidae, rarely or never visit flowers. Hence, the degree of actual specialization in size of *V. peregrina* is at best slight.

Many of the features listed in Table 2 are straightforward and well known, others may require some explanation. Small size (nearly always under 20 g) is common to virtually all specialized avian nectarivores, but within this size range several selective factors can operate: larger size favors social dominance, but reduces the number of flower species that can be profitably exploited (cf. Lyon, 1976; Wolf et al., 1975); small size may favor utilization of torpor as an energy-saving device (Hainsworth et al., 1977; Brown et al., 1978). With regard to locomotion, hovering ability is probably the ultimate specialization in that it permits exploitation of free-hanging blossoms, which give the greatest protection against insect visitation (Faegri & van der Pijl, 1966). However, for nonhovering species, the ability to cling acrobatically to flowers and inflorescences might be manifested in terms of larger feet than nonnectarivorous relatives, especially if these are

typical foliage-gleaning types. In the hummingbirds, where most species hover to feed, the ability to perch while feeding might reduce the costs of nectar extraction, especially for larger species (Wolf et al., 1972, 1975). I know of no small (<4 g) hummingbird that regularly clings to flowers to feed, but many medium-to-large species do, especially in the highlands (Wolf et al., 1976; Stiles, unpublished data). It is probably no coincidence that *Eutoxeres* spp., by far the largest hermit hummingbirds (10–13 vs. 2½–7 g), are also the only ones to regularly cling to flowers to feed and have extraordinarily powerful feet.

The nasal operculum is a fleshy flap that largely covers the nostrils in nectar-feeders; it presumably prevents nectar and pollen from clogging the nasal passages. It may serve as an index of nectarivory in some cases, such as the Coerebidae: it is highly developed in *Diglossa* and *Coereba,* which are highly nectarivorous; and but slightly developed in most other members of the family, who are but occasional, facultative nectarivores (see below).

The bills of nectarivorous birds are important not only as indicators of flower-feeding *per se*; they also reflect the manner of nectar extraction (e.g., whether by piercing, mashing or probing), as well as the diversity and specificity of bird-flower coadaptations that may occur within a region or community—and indirectly, the relative age of the bird-flower association there (e.g., comparing North American vs. neotropical bird-flower communities: cf. Snow & Snow, 1972, 1980; Brown & Kodric-Brown, 1979). However, low bill-flower diversity may exist in a relatively old bird-flower association if specificity *per se* is not highly advantageous (see below and Paton & Ford, 1977).

Specializations of the gut for nectar-feeding are relatively clear-cut, although in such groups as the Dicaeidae, adaptations for nectarivory may overlap with, or be subordinate to, those for frugivory (Docters van Leeuwen, 1954). Brush-tipped tongues occur in several groups that feed on fruit juices as well as (or instead of) nectar (e.g., the Zosteropidae and Coerebidae). No particular gross morphological specialization appears in the gut of the Loriinae: the nectar taken is mainly absorbed in the crop (present in parrots generally), and pollen digestion appears within the capacities of the usual psittacine gut apparatus (Churchill & Christensen, 1970; Forshaw, 1973), although enzymatic specializations may exist. I know of no features of plumage or integument that could be unequivocally interpreted as specializations for flower visitation: feathers in general have an ideal texture for pollen transport (Faegri & van der Pijl, 1966). The bright colors of some (but by no means all) nectar-feeding birds may have evolved in part as aggressive signals in relation to feeding territories, but there is little to suggest that they have evolved to match the flowers they feed on; if anything, the reverse may be true in some cases (e.g., Morton, 1979).

It is precisely in evaluating behavioral specialization for flower feeding that one encounters the greatest difficulties: not only is there much variation between and among different groups, but critical data are scarce or lacking in many cases. The ecological characteristics of flowers as a food source—stationary, conspicuous, renewable, more or less repeatable from one year to the next—allow some deductions about possible behavioral specializations. The aggressiveness and frequent feeding territoriality of nectar-feeding birds follow from these features (Gill, 1971; Stiles, 1973; Carpenter, 1978; Wolf & Wolf, 1976, etc.). By contrast, rela-

tively few data are available on spatial memory of nectarivores, especially in relation to other birds (Gass, 1978). Flower-feeding does not seem to be correlated with promiscuous or polygynous mating systems, contrary to my earlier prediction based upon hummingbirds (Stiles, 1973). Rather, the kinds of social behavior (flocking vs. solitary, monogamous vs. promiscuous, etc.) may affect foraging patterns and thus selection for bird pollination in plants of different phenologies and growth habits (see below and Stiles, 1978b).

THE MAJOR GROUPS OF FLOWER-VISITING BIRDS

Table 3 represents an attempt to compare semiquantitatively the principal groups of flower-feeding birds in terms of their degree of specialization for (and dependence upon) a nectar (or pollen) diet. I use a scale running from 0 = no particular specialization, to 3 = relatively highly specialized, as compared to non-nectarivorous near relatives or putative ancestors (known or hypothetical). The results of this analysis are expressed in terms of an approximate mean degree of specialization for the group in question, and a corresponding figure for the most specialized species in each group. Obviously these figures are an oversimplification: the various criteria used (Table 2) are not necessarily equivalent (at least in any quantitative sense), and specialization in different ways can lead to a similar overall mean. Moreover, the species within each group can exhibit a wide range of specialization according to any given criterion. For many species (indeed, for most species of many groups) published information is inadequate for an accurate assessment of specialization, and the value(s) presented represent simply my best guess. If anything, I have probably been too conservative in judging specialization according to certain criteria (e.g., annual cycles); more detailed study of the group in question might indicate rather a higher degree of specialization than I have assigned (at least for some species). Nevertheless, provided due caution is exercised, I think that these results are useful in comparing the relative specializations of the different groups of nectar-feeding birds, at least to a first approximation. This in turn will facilitate comparison of the total spectra of nectarivorous birds on each continent or major biogeographical region, and the kind and degree of bird-flower coevolution likely within each.

Several conclusions emerge from this analysis. First, by virtually every criterion the hummingbirds are the most specialized avian nectarivores. The most specialized hummingbirds are tightly tied to flowers in nearly every aspect of their biology and are often highly coevolved with a small number of flower species. Such species as *Ensifera ensifera* are totally dependent on specific flower species (in this case, *Passiflora mixta*: Snow & Snow, 1980) for critical energy supplies, just as the flowers require the bird for successful pollination. The extreme degree of bill-corolla exclusiveness in such cases is simply an indication of specialization in numerous other aspects of the biology of bird and plant. Similar but less extreme degrees of specialization are frequent in the group (e.g., Stiles, 1973; Stiles & Wolf, 1979; Wolf & Stiles 1970). Some hummingbird species, although highly dependent upon flowers, obtain nectar almost exclusively by piercing corollas (e.g., *Heliothryx barroti*); thus their potential for forming coevolutionary relationships with particular flower species is low. It is also worth

TABLE 3. Degrees of specialization for flower-feeding of the major groups of flower-visiting birds of the world.[a]

Group (or Representative Specialized Species)[c]	Relative Degree of Specialization (Criteria of Table 2)[b]: Body Size	Bill and Related Structures	Tongue	Digestive Tract	Locomotion	Aggressive, Territorial and/or Foraging Behavior	Annual Cycle	Formation of Specific Coevolutionary Relationships	Mean Overall Specialization	Approx. Maximum Specialization	References
Loriinae (Lories)	1	0–1	3	0–1	0	0	1	0–1	0.81	1.00	8,11,30,31
Trochilidae (Hummingbirds)	3	3	3	3	3	2–3	3	1–3	2.62	3.00	7,14,23–28,36
Meliphagidae (Honeyeaters)	1–2	1–2	2–3	2–3	0–1?	1–3	1–3?	1–2	1.75	2.37	1,7,15,18,27, 30,31,33
Promerops cafer (Cape Sugarbird)	1	2	3	3	0	2	3	3	2.12	—	5,20
Nectariniidae (Sunbirds)	2	2–3	3	3	0–1	2–3	3	2–3	2.37	2.62	1,13,19,21, 27,29
Dicaeidae (Flowerpeckers)	1–2	1	2–3	2	0	0–1	1	2–3	1.31	1.62	1,10,27,33
Zosteropidae (White-eyes)	1–2	1	1–2	0–1	0	0–1	0–2	1	0.87	1.25	1,12,27,31
Zosterops olivaceae (Reunion White-eye)	2	2	2–3	1	0	3	2	2–3	1.87	—	12
Drepanididae (Hawaiian Honeycreepers)	1–2	2–3	2–3	2	0	2+	2+	1–3	1.81	2.13	1,6,7,27,32
Coerebidae (Honeycreepers)	1–2	1–2	2–3	2	0–1	0–2	1–3	0–1	1.43	1.87	2,4,17,22, 24,26
Diglossa baritula (Slaty Flower-piercer)	2	3	3	2	1	2	3	0	2.00	—	22,24,26,34
Icterus (American orioles)	0–1	1	0–2?	0	0	1–2	0–1	1–2	0.62	1.00	3,9,16,26
Icterus spurius (Orchard orioles)	1	1	2?	0	0	2	1	2+	1.12	—	3,9,16,26
Vermivora peregrina (Tennessee warbler)	0–1	0	0	0	0	2	0–1	0–1	0.62	—	26,35

[a] Not included are several small groups for which insufficient data exist to judge specializations: Irenidae, Calleidae (*Philesturnus*), Philepittidae (*Neodrepanis*), etc.; also omitted are numerous families some of whose members take nectar with some regularity, but show little or no specialization for flower-visiting *per se*: Sturnidae, Drongidae, Pycnonotidae, Thraupidae, Parulidae, Fringillidae, etc.

[b] 0 = no particular specialization for flower-feeding (relative to related groups or putative ancestors); 1 = slight specialization; 2 = moderate specialization; 3 = high degree of specialization (dependent upon flowers).

[c] Representative specialized species are often much more specialized than the group as a whole.

[d] References: 1. Austin, 1961; 2. Biaggi, 1955; 3. Beecher, 1950; 4. Beecher, 1951a; 5. Broekhuysen, 1959; 6. Carpenter, 1976b; 7. Carpenter, 1978; 8. Churchill & Christenson, 1970; 9. Cruden & Toledo, 1977; 10. Docters van Leeuwen, 1954; 11. Forshaw, 1973; 12. Gill, 1971; 13. Gill & Wolf, 1975; 14. Hainsworth, 1973; 15. Keast, 1968; 16. Morton, 1980; 17. Moynihan, 1963; 18. Officer, 1964; 19. Schlamowitz et al., 1976; 20. Skead, 1963; 21. Skead, 1967; 22. Skutch, 1962; 23. Skutch, 1975; 24. Snow & Snow, 1971; 25. Stiles, 1973; 26. Stiles, pers. obs.; 27. Thomson, 1964; 28. Wolf, 1970; 29. Wolf & Wolf, 1976; 30. Paton & Ford, 1977; 31. Ford et al., 1979; 32. Raikow, 1976; 33. Terborgh & Diamond, 1970; 34. Lyon & Chadek, 1971; 35. Tramer & Kemp, 1979; 36. Snow & Snow, 1980.

emphasizing that bill-corolla morphologies are useful, but hardly infallible guides to bird-flower coevolution. Extreme bill types need not always indicate highly exclusive relationships: consider those species of *Heliconia* (the "*pogonantha* group" of Stiles, 1979) that show a rather high degree of morphological coadaptation with the Sicklebills (*Eutoxeres* spp.), yet are often pollinated mostly by—and are often critical food resources for—hermits of the genus *Phaethornis* (Stiles & Wolf, 1979). Conversely, some hummingbirds of relatively generalized bill type (straight, ca. 20 mm long) can become quite highly coevolved with particular flowers by virtue of their ecological situation (e.g., Stiles, 1973; Wolf et al., 1976). Thus a realistic evaluation of bird-flower coevolution often requires detailed ecological data, and these are available for relatively few groups.

In most respects the sunbirds (Nectariniidae) qualify as the next most highly specialized group of avian nectarivores. The spate of recent studies on sunbirds by Wolf, Gill, and their coworkers in Africa have demonstrated that these birds are highly adapted for flower visitation in many aspects of their foraging and aggressive behavior (e.g., Gill & Wolf, 1975, 1977, 1978; Wolf et al., 1975). Information on breeding and annual cycles is relatively sparse, but tends to indicate that at least some species approach the degree of specialization in many hummingbirds (cf. Skead, 1967; Wolf & Wolf, 1976, and included references). However, there appear to be few highly exclusive coevolutionary relationships between specific sunbird species and flowers. Most sunbird-flowers can be exploited and pollinated by several sunbird species (Skead, 1967; Gill & Wolf, 1978). Possible exceptions include certain high montane sunbird-*Lobelia* associations (cf. Chapin, 1954) and the *Arachnothera-Musa superba* association in India. In the latter instance, the very long-billed, dull-colored *Arachnothera* sunbirds evidently pollinate widely dispersed riparian clumps of *Musa* in almost exactly the same manner as hermit hummingbirds pollinate certain species of *Heliconia* (P. Davidar, pers. comm.; cf. Stiles, 1975, and below).

Slightly less specialized overall are the honeyeaters (Meliphagidae), but within this group there is a wide range of variation, from species as specialized as most sunbirds (e.g., *Promerops* spp., *Philydonyris novaehollandae*: Broekhuysen, 1959; Paton & Ford, 1977) to a number of species that rarely or never visit flowers at all (Officer, 1964). It is thought that Australia was originally colonized by a slightly to moderately specialized nectarivore stock, which subsequently radiated to fill many nonnectarivore niches in a depauperate avifauna (Austin, 1961; Keast, 1976). A great range of adaptations also occur in the monophyletic Drepanididae of Hawaii, from highly specialized nectarivores to species adapted to a variety of totally different niches. In this case the ancestral form was probably a cardueline finch, and the highly specialized nectarivores represent an end point, rather than a starting point of diversification. Unfortunately, the most specialized Hawaiian nectarivores (*Drepanis* spp.) are now extinct (cf. Amadon, 1950; Baldwin, 1952; Carpenter, 1976b, 1978; Raikow, 1976). The case of the Dicaeidae is exceptional, as many species have evidently formed a tight coevolutionary relationship with certain mistletoes, involving not only pollination but also seed dispersal; adaptations to the latter appear to have taken precedence over those to the former (Docters van Leeuwen, 1954). In no other case known to me are the pollinators of a plant also its regular dispersers.

The coerebids or honeycreepers are a polyphyletic group, some members of which are probably descended from emberizine finches (the genus *Diglossa,* the flower-piercers), some from the tanagers (*Dacnis, Chlorophanes,* and related genera), perhaps some from the wood-warblers; the Bananaquit (*Coereba*) is of uncertain affinities (Beecher, 1951b; Skutch, 1962; R. W. Storer, pers. comm.). The most highly nectarivorous members of the group (*Diglossa, Coereba*) are quite highly specialized and dependent upon floral nectar as an energy source, but they are essentially parasites on hummingbird-flower systems, usually (*Coereba*) or virtually always (*Diglossa*) piercing the corollas of the flowers they visit (e.g., Colwell, 1973; Colwell et al., 1974). *Coereba* is a legitimate pollinator of a few plant species (Feinsinger et al., 1979). The remainder of the Coerebidae are at best facultative nectarivores whose staple foods are insects and fruit (Skutch, 1962; Snow & Snow, 1971; pers. obs.).

Because of their flower-destroying tendencies, the lories can perhaps best be regarded (at least in part) as parasites on coevolutionary relationships between flowers and honeyeaters or sunbirds. The parrots as a whole (at least in the New World) are endosperm specialists, which have evolved as specialized parasites on (mostly) animal-mediated seed dispersal systems; the lories appear to have shifted this general way of life over to flower visitation. Nevertheless, lories may accomplish some "mess and soil" pollination, especially of *Eucalyptus* (Paton & Ford, 1977; Ford et al., 1979).

A number of avian families show a relatively low (perhaps incipient?) degree of specialization for flower-feeding, at least in some species. The white-eyes (*Zosteropidae*) and American orioles (*Icterus,* Icteridae) are typical: most species are generalists, taking much fruit and insects as well as varying amounts of nectar. However, a few white-eyes are markedly more closely associated with flowers than the rest, approaching some sunbirds in degree of specialization (Gill, 1971). Some species of *Icterus* are the major pollinators of certain plant species (e.g., Cruden & Toledo, 1977). Other families contain a sprinkling of species that are behaviorally, but not morphologically, slightly to moderately specialized for flower visitation (e.g., *Vermivora peregrina* of the Parulidae, see above; also certain members of the Sturnidae (Starlings), Dicruridae (Drongos), Irenidae (Leafbirds), Pycnonotidae (Bulbuls), Thraupidae (Tanagers), etc.). Finally, there is a large number of families for which scattered reports of flower visitation exist, but for which there is no indication that nectar is important in their diets, or that they are in any way specialized for acquiring it. These species have little importance in bird-flower coevolutionary systems and will not be discussed further here (although collectively they may play some role in pollination of very generalized brush or "cornucopia" flowers, cf. Faegri & van der Pijl, 1966).

A Geographical Survey of Bird-Flower Coevolution

At the level of zoogeographical regions, the Neotropical undoubtedly contains the most highly specialized, as well as the largest (over 300 species in the Trochilidae alone) assemblage of flower-feeding birds (Table 4). Each of the Paleotropical realms contains perhaps 100–150 species of passerine nectarivores, many of which are at most only slightly specialized. The Ethiopian region contains the

TABLE 4. Nectar-feeding bird assemblages of different zoogeographical regions.

Group	Approximate Number of Species in Region					
	Neotropical	Nearctic	Palaearctic	Ethiopian	Oriental	Australasian
Loriinae (Lories)	0	0	0	0	2	ca. 50
Trochilidae (Hummingbirds)	315	ca. 10	0	0	0	0
Meliphagidae (Honeyeaters)	0	0	0	2	0	160[a]
Philepittidae (False-sunbirds)	0	0	0	2	0	0
Nectariniidae (Sunbirds)	0	0	ca. 5	ca. 60	ca. 35	ca. 13
Chloropseidae (Leafbirds et al.)	0	0	0	0	ca. 10[a]	0
Dicaeidae (Flowerpeckers)	0	0	2	0	ca. 30[a]	ca. 25[a]
Zosteropidae (White-eyes)	0	0	2	ca. 15[a]	ca. 60[a]	ca. 10[a]
Coerebidae (Honeycreepers)	ca. 15[b]	0	0	0	0	0
Icteridae (American orioles and blackbirds)	ca. 20[b]	3+	0	0	0	0
Others[c]	100+	ca. 20	0?	75+	50+	50+

[a] Many of these species are not at all closely associated with flowers and should be considered facultative nectarivores at best, but detailed data not available.

[b] Includes only those species known or suspected to be highly nectarivorous (at least at some phase of their annual cycle).

[c] Includes mostly casual or facultative, and/or unspecialized nectarivores; numbers are mostly rough guesses based upon a variety of casual observations and statements in the literature (e.g., in faunal lists, etc.).

bulk of the rather highly specialized sunbirds and perhaps the most specialized meliphagids (*Promerops*), as well as many species in a variety of families (e.g., Sturnidae, Pycnonotidae, Zosteropidae, etc.) that are considerably less specialized. Several families in the Oriental region contain nectarivorous species, but except for the sunbirds, most would not appear to be highly specialized for flower-visiting. There are virtually no detailed, critical studies of nectar-feeding birds for this entire realm, most of the published information being highly anecdotal in nature. However, it appears to me that this is the tropical region with the smallest assemblage of obligate, highly specialized nectarivores; conversely, there is apparently a relatively large and diverse group of facultative or occasional flower visitors. The collective impacts of these two groups, and the importance of bird pollination in the region as a whole, remain to be evaluated critically. The Australasian region contains virtually the entire large family Meliphagidae, but at most half of these are strongly associated with flowers (Officer, 1964; see also Ford et al., 1979). Also occurring here are the primarily pollen-feeding Loriinae, and a few species of sunbirds and dicaeids. Particularly in New Guinea, a number of species of other groups may be occasionally associated with flowers, but the dominant groups (in terms of numbers of species) in both New Guinea and Australia are the honeyeaters and lories (Terborgh & Diamond, 1970; Paton & Ford, 1977). The Nearctic realm contains a small contingent of hummingbirds obviously derived recently from the Neotropical; it also contains a number of migratory species (*Icterus*, certain Parulidae like *Vermivora peregrina*) that are seldom or never associated with flowers on their breeding areas, but which migrate during the nonbreeding season to the Neotropical realm where they may be quite nectarivorous. Finally nearly the entire Palaearctic realm has

no native flower-visiting birds or bird-pollinated flowers (this was doubtless responsible for the long controversy in the European literature regarding the existence of bird pollination). A few nectarivorous birds do occur in peripheral areas of this region (the Middle East, east Asia).

The two regions for which the most detailed information on bird-flower coadaptations exists are the Neotropical and the Australasian. Bird-flower communities have evidently evolved along radically different lines in these two areas, and it seems instructive to compare the ecological roles of bird pollination systems therein. It should be mentioned at the outset that detailed data are available for only a few communities in each region; however, the patterns within regions seem to be sufficiently consistent, and differences between regions sufficiently pronounced, that the general conclusions I draw should be valid. For the Australasian region I rely mainly on the studies by Recher (1971, 1977), Ford & Paton (1976a, 1976b), Paton & Ford (1977), Ford et al. (1979), Carpenter (1978), Collins (1980), and Hopper & Brundage (1978), with Terborgh and Diamond (1970) being the only really useful reference for New Guinea. For the Neotropical region my main sources are Skutch (1962), Snow & Snow (1971, 1972, 1980), Cruden & Toledo (1977), Toledo (1975a, 1975b), Feinsinger (1976, 1978), Wolf (1970), Wolf et al. (1976), and Stiles (1973, 1975, 1978a, 1978b, 1980, and unpublished data).

In the Australian region birds are often important pollinators of major vegetation types—although in some communities their importance has perhaps been exaggerated in the past. Many of the flowers they visit and often pollinate occur in large, rich, dense patches (e.g., large trees like *Eucalyptus*, dense clumps like *Anizognathus*). Nectar is often extremely abundant locally, so much so that the birds present cannot come near to exhausting it. In such sites (e.g., *Protea* heath) the major pollinators may actually be nonflying mammals (Carpenter, 1978; see also Sussman & Raven, 1978). Between these nectar flushes may be long periods of low nectar availability; many of the birds are nomadic and their movements are tied to blooming periods of major food plants. Breeding of the birds may be tied to nectar supplies, or—especially for the larger species—limited by insect availability. The birds are in general social: most honeyeaters and lories move in groups or flocks, usually traveling between large, transient resource patches.

Perhaps the most striking characteristic of the bird-flower system in Australia is the lack of specificity: as Paton and Ford put it, the birds seem adapted to the flora as a whole, the plants to the Meliphagidae as a whole. Most nectar-feeding honeyeaters of an area are capable of pollinating most of the ornithophilous flowers of the area. The majority of these flowers are of the brush type, with its inherently low filtering ability; this permits mammals to play a major role as pollinators in some cases. Tubular flowers are by no means rare, but the tubes are short, often of the "gullet" type with lateral slits, such that the nectar is accessible to birds with a wide range of bill lengths (Ford et al., 1979). This lack of specificity may be related to the dry, unpredictable climate of much of Australia: at any given site the timing and intensity of flowering may vary greatly from year to year, and the birds evidently track flowering bursts only approximately.

Where flower specificity occurs in Australian plants, it appears more in those flowers with tubular corollas like *Anizognathus* spp. Hopper & Brundage (1978)

found that individuals of the common pollinator of two species of *Anizognathus* (the meliphagid *Anthochaera carunculata*) showed 97% fidelity to each species, but this reflected mainly temporal differences in peak blooming periods and different flower placement, such that different techniques were required to exploit each species. However, there was no suggestion that different honeyeater species were visiting different flower species.

This general picture seems to hold in New Guinea also: different species of flowering trees attract essentially the same spectrum of avian visitors. The birds partition the floral resources according to height, density, and location on the trees, rather than by tree species. This system would well repay further study with marked birds and controlled pollinations. The fact that the overall bird-flower system in wet, tropical New Guinea resembles more the situation in dry subtropical Australia rather than that in wet neotropical areas doubtless reflects in part differing taxonomic affinities and social systems of the birds; but more data are clearly needed before a detailed explanation should be attempted.

The situation in Africa seems to resemble that in the Australasian region in many respects: floral resources occur in large patches that are exploited by several species, at least at some times of the year. However, dominance interactions and territoriality, as well as differences in foraging efficiency, may play more of a role in structuring avian exploitation of the mostly tubular flowers (Gill & Wolf, 1978). However, more detailed studies over the entire annual cycle are definitely needed.

Neotropical bird-flower communities are structured along very different lines than those of Australasia. This region is especially interesting in that it contains several groups of flower-feeding birds that differ strikingly in several aspects of their biology. The dominant group numerically and ecologically is the hummingbirds. The coerebids represent a later addition to the hummingbird-flower systems that may affect the operation of these systems, especially in highland areas (cf. Colwell, 1973; Lyon & Chadek, 1971; Colwell et al., 1974). Finally, still more recent additions include a group of relatively unspecialized passerine nectarivores that may be important pollinators in some situations, and appear to be the closest ecological equivalents to many Old World groups (e.g., many meliphagids, White-eyes, etc.).

The hummingbirds are divided into two subfamilies: the hermits (Phaethorninae) and the typical hummingbirds or nonhermits (Trochilinae), which comprise ca. 90% of the family. Most hermits have long, curved bills and tend to forage at scattered flowers with long, curved, tubular corollas and high nectar flow. Such flowers are usually visited and pollinated exclusively by hermits which partition the different species largely according to microhabitat; the long curved corollas are difficult for most nonhermits to negotiate efficiently. Different hermit flowers often place pollen on different parts of the bird, and have temporally offset flowering seasons.

The nonhermit group is considerably more varied, but one may distinguish three major morphological types: medium-sized (3½–7 g) species with straight bills around 20 mm long; small, short-billed species (mostly under 3½ g with 10–15 mm bills); and a smaller number of species with long (>30 mm) and/or curved bills, medium to large in size (5½–12 g). Obviously not all of the nearly

300 nonhermits will fit neatly into these three types, but at least in Central America the great majority do.

The greatest number of nonhermit species usually falls in the first group in any given community. The amount of morphological divergence between sympatric species is often relatively slight, but even so may have a pronounced effect upon foraging efficiencies and flower choice (e.g., Table 1). Specificity of flower choice is further enhanced by dominance interactions and territoriality, as well as differences in microhabitat in some cases. However, hummingbirds of this type often partition floral resources as much by patch size or flower density as by flower species *per se*: often two or more species of hummingbird are alternate pollinators of a given flower species. The nonhermits of the second group tend to be excluded from many of the flowers exploited by the first group due either to their subordinate status, or their inability to forage efficiently due to their relatively short bills. These small hummingbirds often visit small, short-corolla flowers with nectar production too low to attract larger and more dominant species; they often share the role of pollinators with insects like butterflies or bees. The members of the third group of nonhermits often resemble hermits in their foraging, visiting flowers with long and/or curved corollas that often are scattered in small patches. These hummingbirds are most prominent in microhabitats or regions where the true hermits are scarce or absent: the canopy of wet lowland forest, dry forest, or at high elevations. Like the hermits, they may also be exclusive pollinators of some plant species by virtue of morphology.

Overall, there is thus a considerable degree of specificity of flower choice in hummingbird-flower communities—at least at the the level of the morphological type of hummingbird, if not always at the level of species. Any given plant species usually receives a great majority of visits from one or a very few hummingbirds, representing a relatively small proportion of the total number of hummingbird species present. Therefore, compared with a honeyeater-flower community, one might expect greater species richness in hummingbird-flower communities. Certainly the ratio of flower species to bird species seems higher in the latter: for instance, at Finca La Selva, Costa Rica (Table 6) occur some 20 species of hummingbirds, and approximately 50 species of plants are pollinated mostly or exclusively by them. By contrast, some 21 species of ornithophilous plants near Adelaide, Australia were visited and pollinated by 25–28 species of birds (Paton & Ford, 1977). Overall, Ford et al. (1979) estimate that over 100 species of birds have been recorded as visiting the flowers of some 250 plant species in Australia. In Costa Rica alone, I have records of ca. 75 species of birds visiting the flowers of over 300 species of plants. About 55 of the birds can be considered regular flower visitors, and well over half of the plants are probably pollinated mostly or exclusively by birds (taxonomic uncertainties and lack of detailed information on pollination prevent me from venturing more precise estimates of plant species numbers).

One other geographical pattern deserves mention. In the New World, the vast majority of ornithophilous plants are herbs, shrubs, small trees, or epiphytes; very few are canopy trees. Only one out of nearly 50 hummingbird-pollinated plants at Finca La Selva is a canopy tree (*Erythrina cochleata,* which has a very small crown with sparse branching and few flowers). No trees are pollinated by

hummingbirds in a Costa Rican montane site (Wolf et al., 1976) or a California mountain area (Stiles, 1973). By contrast, many ornithophilous plants of the Old World are trees (e.g., Chapin 1954; Officer, 1964; Skead, 1967; Paton & Ford, 1977) which often form the dominant vegetation over sizeable regions (Ford et al., 1979). I think this relates to the social systems of the common flower-birds of these areas: passerine nectarivores (and lories) of the Old World tend to travel in groups or flocks, whereas hummingbirds are virtually always solitary. A large concentration of flowers, as on a large tree, would quickly be parceled up into individual feeding territories by hummingbirds (e.g., Stiles & Wolf, 1970), which could drastically reduce cross-pollination. However, the nectar resources of even a large tree could be exhausted fairly quickly by a flock of larger passerine nectarivores, which would then have to move on to the next tree—thereby effecting cross-pollination.

The role of the relatively unspecialized, recently derived passerine nectarivores of the New World—e.g., *Icterus* spp., possibly even the Tennessee Warbler *Vermivora peregrina*—is of particular interest in this connection. Many of the species of plants pollinated by these birds are large trees with abundant flowers, e.g., *Erythrina poeppigiana* and *E. fusca* (Feinsinger et al., 1979; Morton, 1979; see also Cruden & Toledo, 1977). Like Old World nectarivores, these species tend to move in groups or flocks—indeed, in appearance and behavior the Tennessee Warbler on its tropical wintering grounds seems to be the exact equivalent of a White-eye! Moreover, several ornithophilous brush-flowers of the New World are pollinated by these passerine nectarivores rather than hummingbirds (e.g., *Combretum farinosum*; Alvarez del Toro, 1963). It is also worth noting that many species of nectarivorous bats also forage in flocks, that the plants that they pollinate are often trees, and that the flowers involved are often brush-flowers (Heithaus et al., 1974).

EVOLUTIONARY PATTERNS, WITH EMPHASIS ON THE NEOTROPICS

The earliest flowering plants were probably pollinated by primitive pollen-eating insects, probably beetles (Baker & Hurd, 1968; Faegri & van der Pijl, 1966). Just how and when such a pollination system incorporated nectar as an attractant, and specialized insects and finally birds as pollinators is highly speculative. The early fossil record of flowers and their pollinators is decidedly scanty, but we do know that specialized flower-visiting bees and essentially modern bats were present by the early- to mid-Tertiary (Baker & Hurd, 1968; Raven & Sussman, 1978). Flower-visiting birds *per se* do not appear in the fossil record until the Pleistocene (cf. Thomson, 1964) but undoubtedly originated considerably earlier. The taxonomic distinctness of the specialized avian nectarivores of the Neotropical, Ethiopian, and Australasian regions (Table 3) suggest that flower-feeding as a way of life originated independently in each well after their separation by continental drift. Africa and South America share no nectar-feeding groups, and were separated by a water gap sometime in the Cretaceous (cf. Baker, 1973). Therefore, the story of bird-flower coevolution begins probably sometime in the early- to mid-Tertiary. Given that the hummingbirds are the largest, most taxonomically distinct, and most specialized group of flower-birds, it seems not un-

likely that bird-flower coevolution began relatively earlier in the New World than elsewhere.

The early evolution of the hummingbirds is shrouded in mystery, and even their affinities among modern birds remain in doubt. Hummingbirds have usually been placed in the same order as the swifts because of similarities in their flight mechanism (and small feet). However, recent morphological studies (J. Cohn, R. Zusi, pers. comm.) indicate that these similarities are most likely due to convergence; certainly hummingbirds and swifts fly rather differently. Like Skutch (1975), I find it much easier to envision the evolution of hummingbirds from a passerinelike, rather than a "primitive swiftlike" (cf. Austin, 1961) progenitor. The evolution of a bill and tongue specialized for nectar-feeding from the reduced structures adapted for aerial insect-feeding as practiced by swifts, swallows, etc., seems most unlikely. Rather, the "proto-hummingbird" might have been a small, sallying and hover-gleaning insectivore not unlike some modern parulids (e.g., Morse, 1967), that would have sought its food in the foliage (and possibly flowers) at the tips of twigs. A progressive emphasis on hovering and the concomitant decline in the role of the legs could have led to reduction of the latter. Small legs and feet that are little used in foraging occur not only in swifts and other aerial insectivores, but also—and more to the point—in specialized sally-feeders (jacamars, motmots, puffbirds, etc.) that clearly did not evolve from "swiftlike" ancestors. While it is generally agreed that the earliest visits of birds to flowers were for insects (Faegri & van der Pijl, 1966), it is worth noting that bees (and presumably nectar-containing bee flowers) were present by the time the hummingbirds presumably were evolving. These birds may have been specifically associated with nectar from the first.

Pollination by hummingbirds has long been established in the neotropics as evidenced by the families (e.g., Musaceae, Bromeliaceae) and large genera (e.g., *Cavendishia, Costus, Columnea, Aphelandra*) that are largely or entirely hummingbird-pollinated there. Insect (bee or lepidopteran) pollination was probably the precursor of hummingbird pollination, not only because these insects were first on the scene but because intermediate stages of the process are visible today. For example, the genus *Costus* contains many bird-pollinated species (with red or yellow flowers and/or bracts, narrow corolla tube, high nectar production) and bee-pollinated species (usually green bracts, whitish flowers with yellow or purple "nectar guides," low nectar production, broad campanulate corolla tube). *Costus malortieanus* of Costa Rica resembles bee-pollinated species in color but has an intermediate corolla tube and high nectar production; it is pollinated both by hermit hummingbirds and *Eulaema* bees (Stiles, 1978a; Stiles & Wolf, 1979; H. Kennedy, pers. comm.). Another example is *Hamelia* of the Rubiaceae, a family usually associated with lepidopteran pollination. This genus contains species pollinated by birds, butterflies, or both (pers. obs.; Opler, 1981).

EVOLUTION OF THE PHAETHORNINAE AND TROCHILINAE AND THEIR FLOWERS

Plant-pollinator relationships may also help to shed some light on the evolution of the two subfamilies of hummingbirds, the hermits and nonhermits (see above).

TABLE 5. Altitudinal distributions of hermit (Phaethorninae) and "typical" (Trochilinae) hummingbirds in three New World areas.

	Numbers of Species				
Area and Subfamily	Tropical	Premontane	Lower Montane	Montane + Subalpine	Total Species[a]
A. Costa Rica[b]					
Phaethorninae	5	3	1	0	6
Trochilinae	20	24	12	5	45
B. Colombia[c]	Tropical	Subtropical	Temperate	Paramo	
Phaethorninae	20	6	0	0	19
Trochilinae	61	60	38	10	115
C. Venezuela[d]					
Phaethorninae	13	2	0	0	13
Trochilinae	59	47	24	7	84

[a] Less than the total of altitudinal zones, as many species occur in more than one altitudinal zone. However, species that barely enter a zone, or do so only rarely, are *not* counted for that zone.
[b] From Slud (1964) and personal observations. Altitudinal zonation based on Holdridge life zone system.
[c] From de Schauensee (1960); altitudinal zonation that of Chapman, which compares with Holdridge system as follows: "Tropical" includes much of premontane; "Subtropical" includes upper premontane, and most of lower montane; "Temperate" is nearly equivalent to montane, but includes uppermost lower montane; paramo and subalpine are essentially equivalent.
[d] From de Schauensee & Phelps (1978); altitudinal zonation is the same as 3.

The hermits are basically birds of the understory of wet tropical forest; they decrease in abundance and diversity towards higher elevations or drier areas (Table 5, Fig. 1), and extend northward only to the limits of lowland "rain" forest in Veracruz, Mexico (Friedmann et al., 1950). By contrast, the nonhermits reach their greatest diversity in the tropical highlands, around 1000–1500 m elevation in Costa Rica (Table 5, Fig. 1). In wet tropical lowlands, nonhermits are most numerous in the forest canopy rather than the understory, at least for most of the year (Stiles, 1978a, 1980). Nonhermits are the most numerous group in dry tropical areas, where the hermits occur only in riparian habitats—if at all. Also, only the Trochilinae reach higher northern latitudes or occur above 2000 m elevation at tropical latitudes (cf. Snow & Snow, 1980; Stiles, pers. obs. and Fig. 1).

Each of these groups appears to have evolved for a long time in conjunction with a particular set of flowers. The hermits are virtually always associated closely with large monocotyledonous herbs of the order Scitamineae, notably the genus *Heliconia* (Table 6; also see Snow & Snow, 1980). At least 34 of the 40 known Costa Rican species of *Heliconia* (Stiles, 1979, and unpublished data) are hermit-pollinated, notably by members of the genus *Phaethornis*. Isolated species in several species-groups have secondarily become adapted for pollination by nonhermits, usually in conjunction with occupying younger second-growth habitats. Neither hermits nor *Heliconia* occur above 2000 m in Central America or northern South America, and only a single nonhermit-pollinated species occurs widely in dry and/or open areas where hermits are absent (Stiles, 1975, 1979).

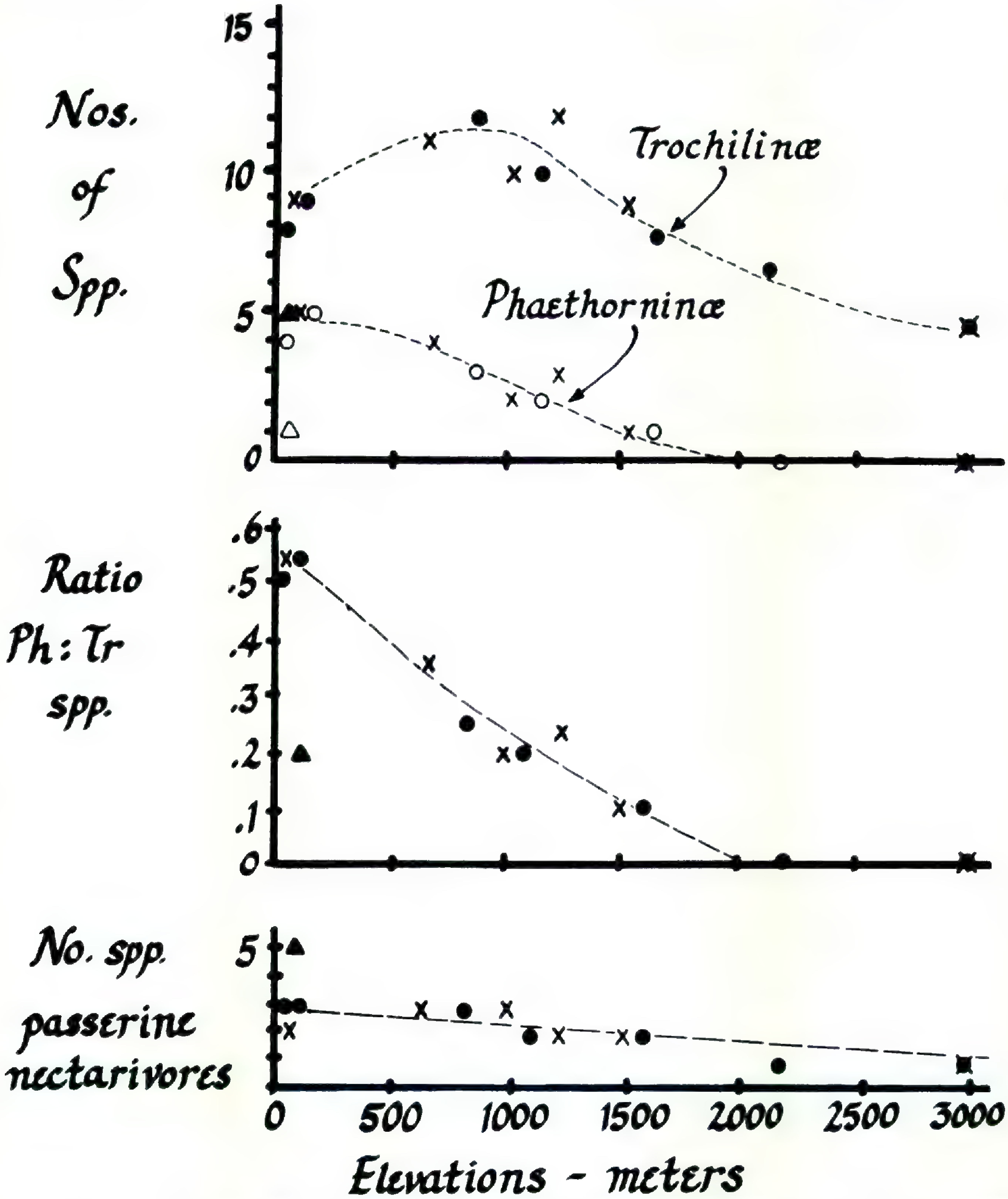

FIGURE 1. Numbers and ratios of species of hermit (Phaethorninae) and "typical" (Trochilinae) hummingbirds, and of passerine nectarivores, that are common and/or resident at 13 sites in Costa Rica at different elevations. Circles = Caribbean slope; crosses = humid Pacific slope; triangles = dry Pacific slope.

Most of the plant groups that are mostly or entirely pollinated by the non-hermits reach their greatest diversity in the tropical highlands, and most are dicots (e.g., the tribes Thibaudeae of the Ericaceae, Fuchsiae of the Onagraceae) (Table 6). The only monocot family showing close association with the Trochilinae is the Bromeliaceae; and these are mostly epiphytes of forest canopy, a habitat rarely exploited by hermits (Stiles, 1980). At Finca La Selva, Costa Rica, the

only bromeliad pollinated by hermits is a terrestrial forest species, *Aechmea magdalenae*. With the possible exception of the Acanthaceae, all the major dicot families have a majority of nonhermit-pollinated species—although most have hermit-pollinated species as well, usually in different genera. The Rubiaceae are especially interesting in this regard: most ornithophilous species of the family have short, straight corolla tubes, clustered flowers, and relatively low nectar production, obviously adapted for nonhermit pollination. The small epiphyte *Ravnia triflora* presents an interesting contrast: the flowers open singly, and they have a very long corolla tube and relatively high nectar production. In effect, in corolla shape and nectar production, most Rubiaceous bird-pollinated flowers show affinities with the many species of the family that are pollinated by butterflies and small sphingids; a few species, like *Ravnia*, appear to resemble those more specialized species pollinated by very large and long-tongued sphingids (cf. Cruden et al., 1981). Thus it may be that the latter species are to some extent preadapted for hermit pollination in a family most of whose avian pollinators are nonhermits.

As noted above, in areas or microhabitats where the hermits are rare or absent, certain species of nonhermits and their flowers have converged on the "hermit-flower" syndrome. Examples in Costa Rica include *Eugenes fulgens* and *Campylopterus hemileucurus* at high elevations, and *Heliomaster* spp. in dry areas or in forest canopy. Where both groups occur together in tropical wet lowlands, the hermits are denizens of forest understory and light gaps; nonhermits occur chiefly in the forest canopy, at larger light gaps, and outside the forest (Slud, 1960; Stiles, 1980).

In the past, the hermits have sometimes been considered primitive (e.g., Ridgway, 1891), perhaps partly due to their lack of brilliant iridescence. I think rather that the ecological and behavioral evidence, in particular the coevolutionary relationships with different flower groups, point to a long period of separate evolution of the two groups. One could even envision the same group of "proto-hummingbirds" giving rise independently to hermits in tropical wet lowlands and to nonhermits in the highlands, during the early to mid-Tertiary. At the present time the center of diversity of the hermits is the Amazon basin, particularly the western portion. The Trochilinae attain their greatest diversity in the Andes, but this undoubtedly reflects the great burst of speciation and differentiation associated with the Pliocene-Pleistocene uplift of the Andes. The actual center of origin of the nonhermits may lie in the much older highlands of eastern Brazil.

HUMMINGBIRD-FLOWER COEVOLUTION IN NORTH AMERICA

Only a small, morphologically homogeneous group of nonhermits (currently classified in four badly oversplit genera) has succeeded in occupying North America well north of Mexico. Several factors suggest that this group has arrived relatively recently in North America and speciated there. Nearly all species are segregated geographically or by habitat during the breeding season; when two species breed in the same habitat, their breeding seasons are temporally offset (Pitelka, 1951; Stiles, 1973). With the exception of the large genus *Castilleja* (which is well represented in Mexico), North American hummingbird flowers

occur as isolated species in otherwise entomophilous genera, or as small and poorly differentiated genera (Grant & Grant, 1968).

The morphological uniformity of the hummingbirds is matched by that of their foodplants. Following their respective breeding seasons, several species of hummingbirds regularly cooccur in mountain meadows of southwestern North America, and several species of hummingbird flowers bloom simultaneously in these habitats (Grant & Grant, 1968; Stiles, 1973). The birds in such assemblages evidently do not discriminate between flower species to any marked degree, and all species of hummingbirds may pollinate any given species of flower; the flowers seem to have converged to a common color and morphology (Brown & Kodric-Brown, 1979). This overall lack of specificity brings to mind the structure of Australian bird-flower communities, rather than the more complex hummingbird-flower communities of the neotropics (see above). It is noteworthy that all North American hummingbirds are (or were, until recently; see Stiles, 1973) migratory. Their seasonal movements, coupled with the dry and variable (on a year-to-year basis) climates of western North America may add an element of unpredictability to the system that has inhibited the evolution of more specific coadaptations: flexibility may be important for both birds and flowers, as it seems to be in Australia. We definitely need more data on interyear variation in the composition and dynamics of these bird-flower assemblages to evaluate this hypothesis.

A number of species of plants in the western North American flora seem to be evolving towards hummingbird pollination, and presently possess more or less brushlike flowers (e.g., *Trichostema lanatum, Isomeris arborea*). Indeed, a "brush" phenotype could be interpreted as the first step towards adaptation to a larger pollinator, to be followed by a lengthened corolla tube and tighter coevolutionary relationships. I have seen *Trichostema* visited and pollinated by both hummingbirds and large bees in California; bee pollination is almost certainly ancestral (Grant & Grant, 1968).

It is of interest that many North American species pollinated by hummingbirds, despite their relatively recent origin, appear in most respects (color, form, amount and sugar composition of nectar) to be as specialized for these pollinators as do most of the evolutionarily older tropical species (Grant & Grant, 1968; Stiles, 1976; Baker & Baker, 1981; Cruden et al., 1981). Only in the higher concentrations of amino acids in the nectars of the former is their more recent origin clearly reflected (Baker & Baker, 1975).

POLLINATION BY PERCHING BIRDS

Pollination by perching birds also appears to be of relatively recent origin in the New World, and may be primarily associated with the family Icteridae (genera *Icterus, Dives, Notiopsar,* etc.) (Toledo, 1975a; Cruden & Toledo, 1977). A range of degrees of specialization for nectar-feeding is evident in the large genus *Icterus* itself (Beecher, 1950), with the most specialized species still considerably less specialized than the major Old World nectarivores (cf. Table 3). Cruden and Toledo compare the New World passerine nectar-feeders as a whole with the facultative and relatively unspecialized Old World nectarivores of such families as the Pycnonotidae, Oriolidae, Sturnidae, etc.

TABLE 6. Taxonomic affinities of hummingbird flowers, in relation to their primary pollinators (Phaethorninae vs. Trochilinae).

	Primary Pollinator	No. Sp. of Monocots				
		Brome-liaceae	Musaceae	Zingi-beraceae	Other	TOTAL
Finca La Selva, Costa Rica	Ph.	1	6	4	1	12
pers. obs. 100 m	Tr.	7	3	1	0	11
La Montura, Costa Rica	Ph.	6	3	2	0	11
pers. obs. 1100 m	Tr.	5	1	1	1+	8+
Villa Mills, Costa Rica pers. obs. 3000 m	Tr.	1	0	0	2+	3+
Santa Rosa, Costa Rica[a] pers. obs. 150 m	Tr.	2	1	0	3	6
Arima Valley, Trinidad	Ph.	4	4	2	1	11
(Snow & Snow, 1972)	Tr.	4	0	0	0	4
Las Tuxtlas, Veracruz, Mexico	Ph.	0	1	2	0	3
(Toledo, 1973)	Tr.	2	1	0	0	3
Sta. Monica Mts. Calif. (Stiles, 1973)	Tr.	0	0	0	0	0
Venezuelan Andes pers. obs. 2000 m+	Tr.	3+	0	1+	1	5+

[a] Includes a single species of hermit, the small (2.5 g), relatively generalized (bill 22 mm, nearly straight) *Phaethornis longuemareus*, which is normally restricted to gallery forest.

Another indication of the recency of passerine pollination is that the flowers involved occur as isolated species in genera adapted for pollination by hummingbirds or other agents (Toledo, 1975a, 1977; Cruden & Toledo, 1977). Passerine pollination is by no means necessarily evolved from hummingbird pollination. Such pollination systems may have evolved from bat-pollinated flowers (e.g., *Agave* and perhaps some Marcgraviaceae; Stiles, unpubl. data), and perhaps other systems as well. The geographical distribution of passerine nectarivores also differs from that of hummingbirds in several respects, leading one to suspect that passerine pollination is often complementary to hummingbird pollination, rather than necessarily evolved from it. In humid life zones there is only a slight decrease in the number of passerine nectarivores with altitude—and most of the latter are members of the family Coerebidae, which only exceptionally are *bona fide* pollinators (Fig. 1). The maximum diversity of passerine nectarivores in Central America occurs in dry tropical lowlands, where hummingbirds are relatively poorly represented (Table 6; see also Wolf, 1970). Conversely, the genus *Icterus* reaches its greatest diversity in the drier areas of Mexico and northern Central America (Beecher, 1950); passerine pollination is probably well established in the American southwest in genera like *Fouquieria* and *Agave* (Stiles, unpubl. data; Toledo, pers. comm.).

CONCLUSION

It is striking that many of the species adapted for passerine pollination appear to be as specialized for these pollinators, and in the same ways (nectar compo-

TABLE 6. Continued.

No. Spp. of Dicots										Total No. Hum-ming-bird food-plants	No. Spp. of Hummingbirds		
Acan-tha-ceae	Eri-caceae	Ges-neri-aceae	Labia-tae	Lobeli-aceae	Ona-gra-ceae	Rubi-aceae	Scroph-ulari-aceae	Other	TOTAL		Com-mon and/or Resi-dent	Rare + Irreg-ular	TOTAL
4	0	1	0	0	0	1	0	2	8	20	5	1	6
2	1	5	0	0	0	4	0	7	19	30	9	7	16
3	0	2	1	1	0	1	0	1+	9+	20+	2	2	4
3	6	7	0	1+	0	3+	0	7+	27+	35+	10	7	17
0	3	0+	2	3	3	0	1	3	15+	1	4	2	6
2	0	0	1	0	0	2	1	6	12	18	5	3[a]	8
1	0	0	0	1	0	0	0	3	5	16	3	0	3
1	0	0	0	0	0	6	0	6	13	17	6	3	9
1	0	1	1	0	0	0	0	0	3	6	2	0	2
2	0	0	0	0	0	2	1	5	10	13	7	2	9
0	1?	0	2+	0	4	0	4	2	12	12	3	3	6
1?	4	2	4	4	4	1	2	5+	27+	31+	—	—	20+

sition, presence of perch, etc.), as are many ornithophilous species in the Old World (Cruden & Toledo, 1977; Cruden et al., 1981; Baker & Baker, 1981). These observations strongly support the hypothesis of Baker & Hurd (1968) regarding plant-pollinator coevolution in general. These authors postulate that the initial selective demand is made by the animal, as an unspecialized flower visitor; the most profound evolutionary response is by the plant, in the form of a suite of adaptations to attract the visitor consistently enough that it becomes a reliable pollinator—in short, a "syndrome" in the classical sense. The behavioral flexibility of the animal thus fits with what might be considered the evolutionary flexibility of the plant—that is, the variety of ways in which genetic variation in plant populations can be rapidly reorganized and selected, via the different mechanisms of rapid speciation in these organisms, including hybridization and polyploidy (Raven, 1980).

Further evolution of the presumptive coadapted complex could occur in various directions discussed in this paper. The pollinator could evolve towards increased specialization for, and dependence upon, floral food (a process just beginning in New World orioles, and virtually completed in the Trochilidae). Selection may favor further elaboration of the reward unit of the plant, not only in terms of filtering mechanisms to restrict reward availability to a particular subset of potential pollinators, but also through controlling the provision of energy to these so as to favor degrees of interplant movement most compatible with the optimal pollination unit (Heinrich & Raven, 1972; Stiles, 1978b). All stages of this evolutionary scenario can be found in the complex of nectarivorous birds and the flowers they visit and pollinate. Bird-flower systems are proving to be a fruitful vehicle for understanding plant-pollinator coevolution in a general sense.

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THE DISTRIBUTIONAL PATTERNS OF NEW WORLD NECTAR-FEEDING BATS[1]

KARL F. KOOPMAN[2]

ABSTRACT

Whereas in the Eastern Hemisphere, all nectar-feeding bats are members of the suborder *Megachiroptera*, in the tropical and subtropical portions of the Western Hemisphere (in the absence of megachiropterans) certain members of one family (Phyllostomidae) of the generally insectivorous suborder *Microchiroptera* have become adapted to nectar feeding. These adaptations involve such diverse areas as skulls, teeth, tongues, throat muscles, and stomach linings. Considerable diversity in these characters may be seen within the New World nectar feeders, dependent in part on whether insects or pollen are the prime protein source. The distributions of all currently recognized recent species (35 in 16 genera) are mapped. Patterns are diverse but with a majority of the genera and many species being widespread on the tropical American mainland. Origin in either South or Middle America and ecological restriction will explain the distributions of some, but for many, causes are still obscure. Of the two currently recognized subfamilies of New World nectar-feeding bats the *Brachyphyllinae* are endemic to the West Indies and have obviously been there for a long time whereas the *Glossophaginae* probably originated in South America and have reached the West Indies much more recently.

While bats were originally strictly insectivorous, many species, particularly in the tropics (where most kinds of bats live), have become adapted for obtaining a variety of food, including fish, terrestrial vertebrates, blood, fruit, and nectar. It is with the nectar-feeders that we will be especially concerned here. Because this radiation is chiefly a tropical phenomenon and since the New and Old World tropics have been separate at least since the beginning of the Miocene, it has proceeded independently in the two hemispheres. In the Eastern hemisphere, the fruit- and nectar-feeders (with the exception of one New Zealand genus) all belong to the suborder Megachiroptera, which combines primitive skull and post-cranial characters with teeth which are highly modified for handling fruit, nectar, and pollen. Some members of this suborder have tongues which are highly specialized for extraction of nectar from flowers. All the insectivorous and carnivorous species belong to another suborder, the Microchiroptera. The members of this group have a number of modifications of the skull and post-cranial skeleton related to the catching of anthropod or vertebrate prey, but their Old World representatives, in general, show little in the way of dental modification.

In the New World tropics, there are no Megachiroptera and no evidence that they ever occurred. In their absence a number of species of one of the endemic Western Hemisphere Microchiropteran families, the Phyllostomidae, have become adapted to feeding on fruit and nectar. Other members of the family feed on insects, terrestrial vertebrates, and blood. In connection with their diversity

[1] Figures 1 and 7–16 were drawn by Ms. Christine Miller. Figures 2–5 were drawn by Dr. Giles MacIntyre and originally appeared in Koopman & MacIntyre (1980). I am indebted to Dr. Donna Howell for Fig. 6. She also, as well as Dr. Guy Musser of this department and Dr. Thomas Griffiths, read and criticized the manuscript.

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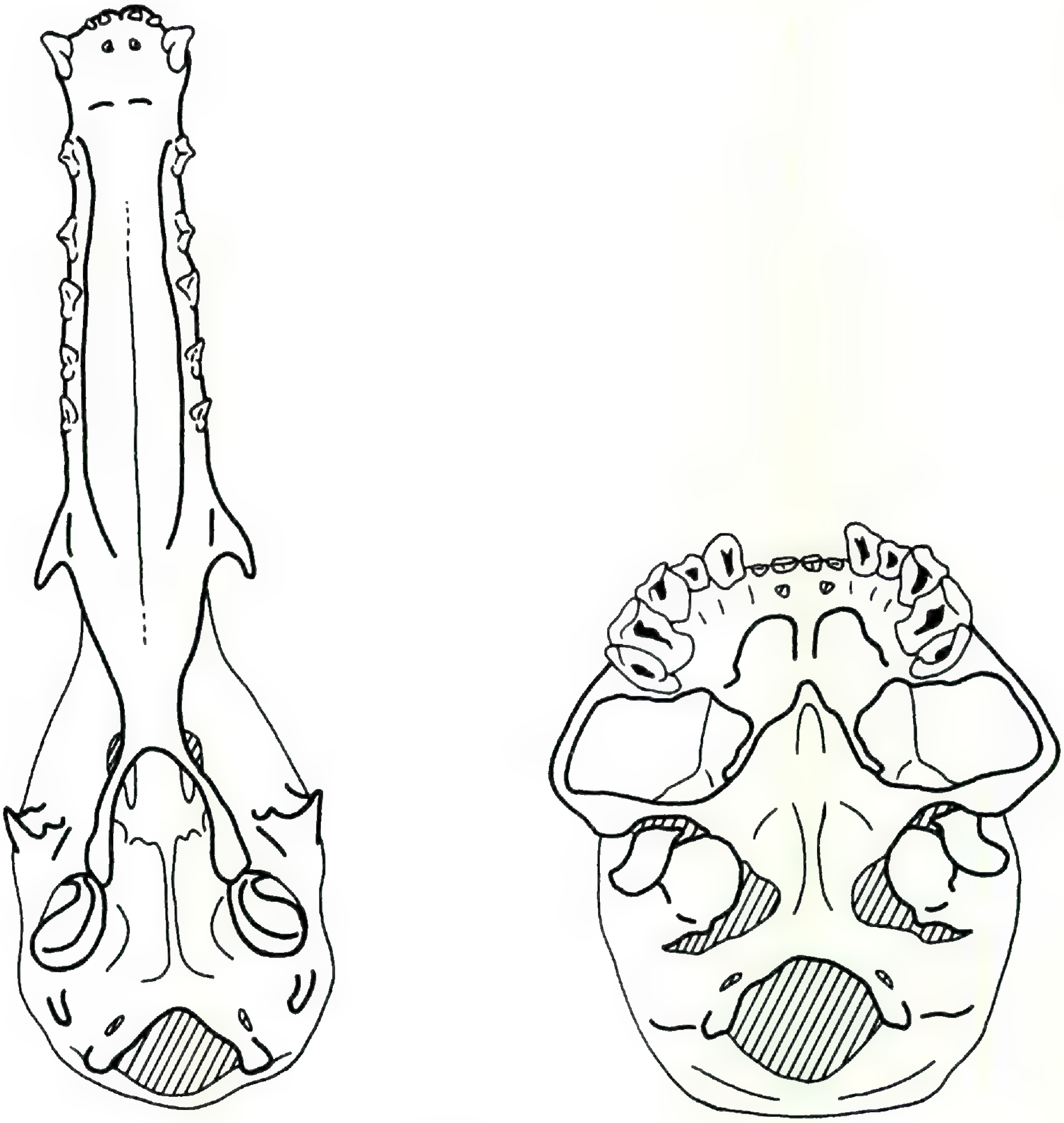
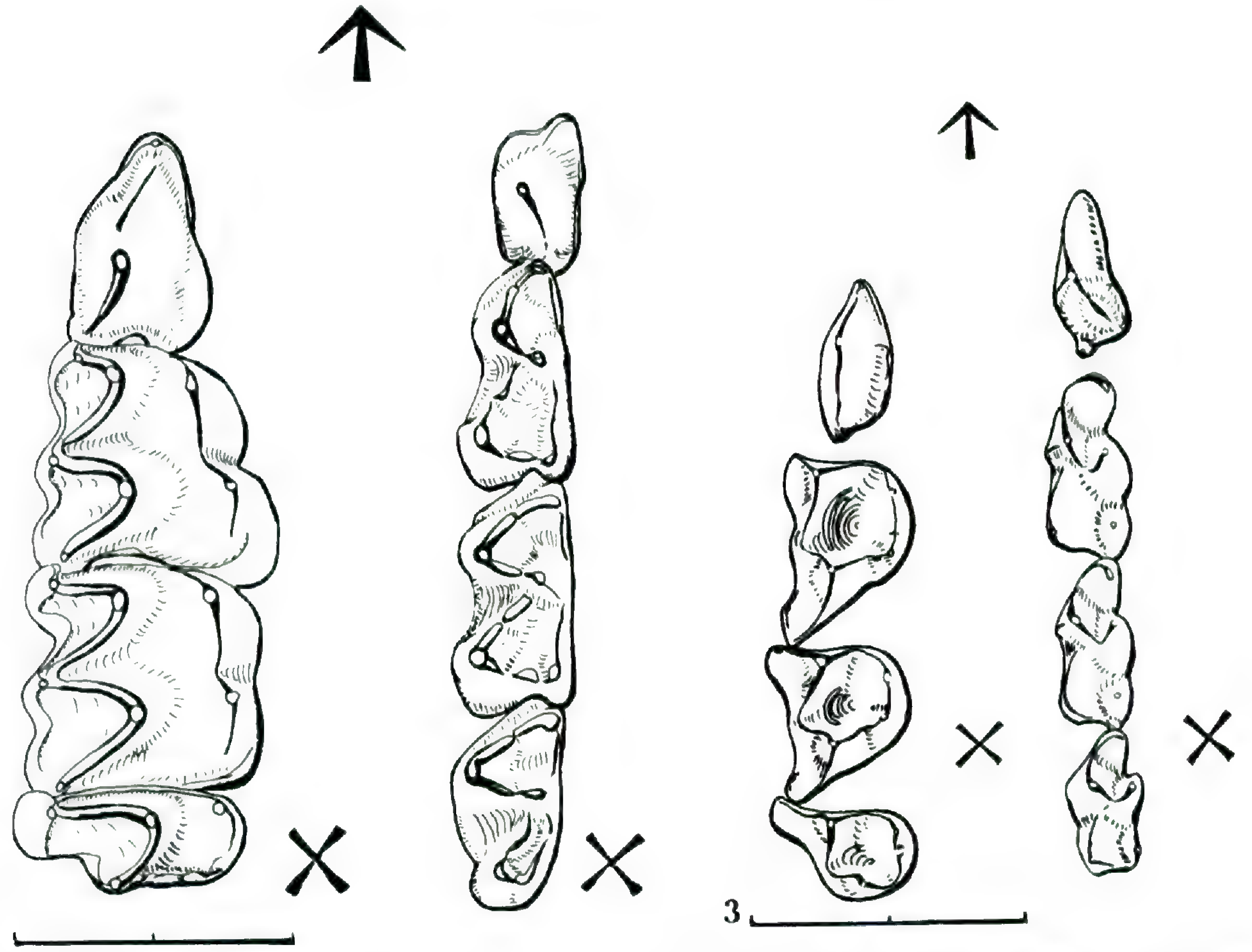


FIGURE 1. Skulls in partial view of two highly specialized phyllostomid bats; *Musonycteris harrisoni* (AMNH-235179) on the left, a nectar feeder; *Centurio senex* (AMNH-179991) on the right, a fruit eater.

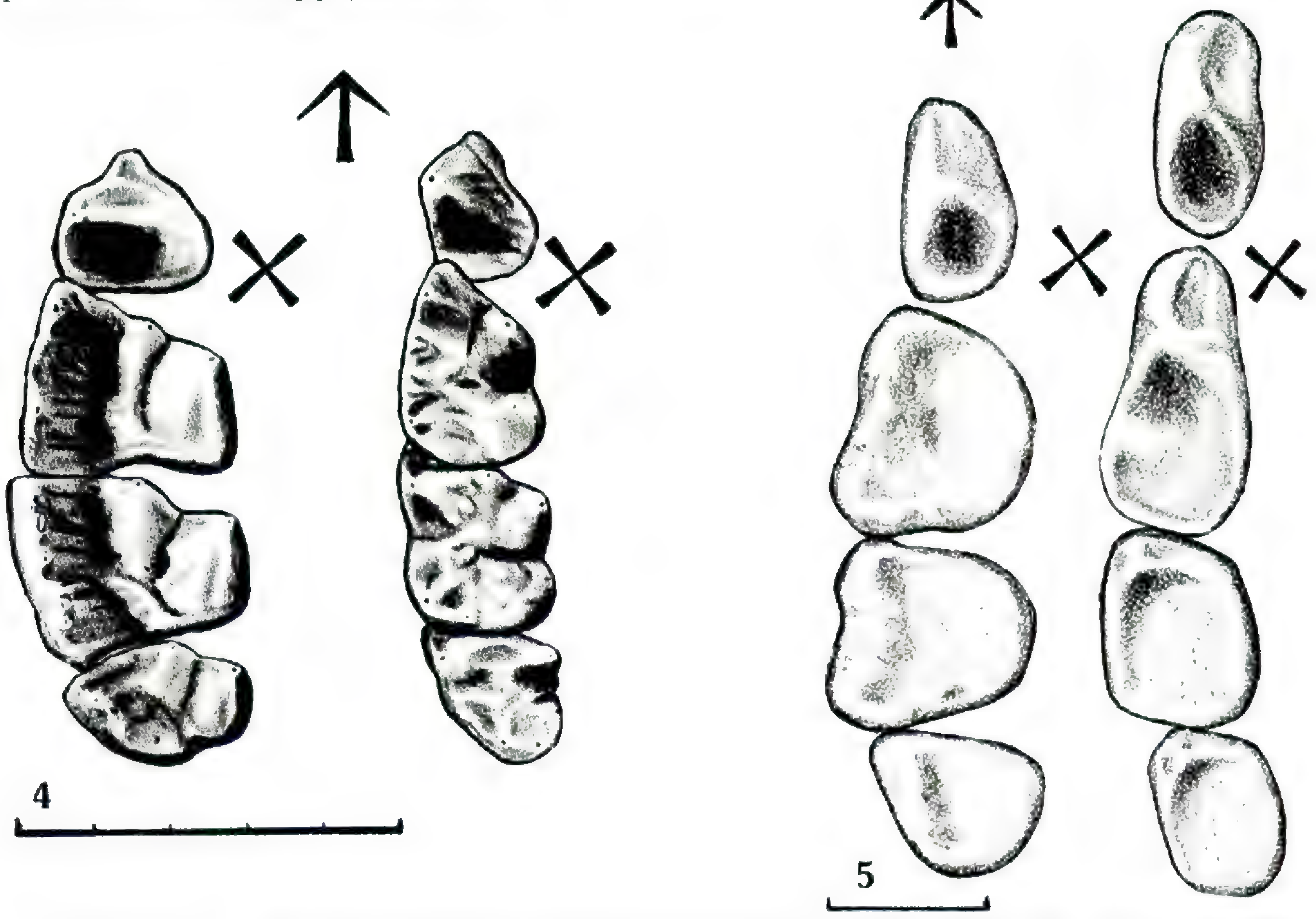
in feeding habits, the Phyllostomidae show an equal diversity in skull, tooth, and tongue morphology, some of which will be briefly discussed here.

In skull proportions, there is a tremendous spread, with a few highly specialized fruit-eaters having skulls which are almost as wide as they are long and with the rostral portion (in front of the braincase) being only about one-third of their total length. On the other hand, one of the most specialized nectar-feeders has a skull length approximately four times its breadth and with the rostral portion constituting about two-thirds of its length (Fig. 1).

Likewise the molar teeth, which in primitive members of the family are well adapted to chopping up insect exoskeletons, become highly modified in more derived species in connection with the various specialized diets, particularly fruit, nectar, and blood (Figs. 2–5). In nectar-feeders, this change involves first a weak-



FIGURES 2–3. Molars and posterior premolars of bats.—2. Upper teeth (left), lower teeth (right) of an insectivorous phyllostomid bat (*Micronycteris*).—3. Upper teeth (left), lower teeth (right) of a primitive nectar-feeding phyllostomid bat (*Glossophaga*).



FIGURES 4–5. Molars and posterior premolars of bats.—4. Upper teeth (left) and lower teeth (right) of a derived fruit and nectar-feeding phyllostomid bat (*Brachyphylla*).—5. Upper teeth (left) and lower teeth (right) of a highly derived nectar-feeding phyllostomid bat (*Phyllonycteris*).

FIGURE 6. Electron-micrograph of a portion of the tongue of *Leptonycteris*. Note the long papillae forming the nectar "mop." Taken from Howell & Hodgkin (1976).

ening (Fig. 3) and eventually a complete degeneration (Fig. 5) of the molar cuspidation. In nectar-feeders, however, the tongue does most of the work of obtaining food. As a result, it is modified in two ways. First, it is lengthened in order to reach the nectaries of flowers and this, of course, is related to the lengthening of the rostral portion of the skull. Second, the tongue papillae are greatly lengthened forming a sort of "mop" for sopping up the nectar (Fig. 6). See Griffiths (1978) for further nectar-feeding modifications of the tongue.

Nectar is a good source of carbohydrate but a poor source of protein. Primitive

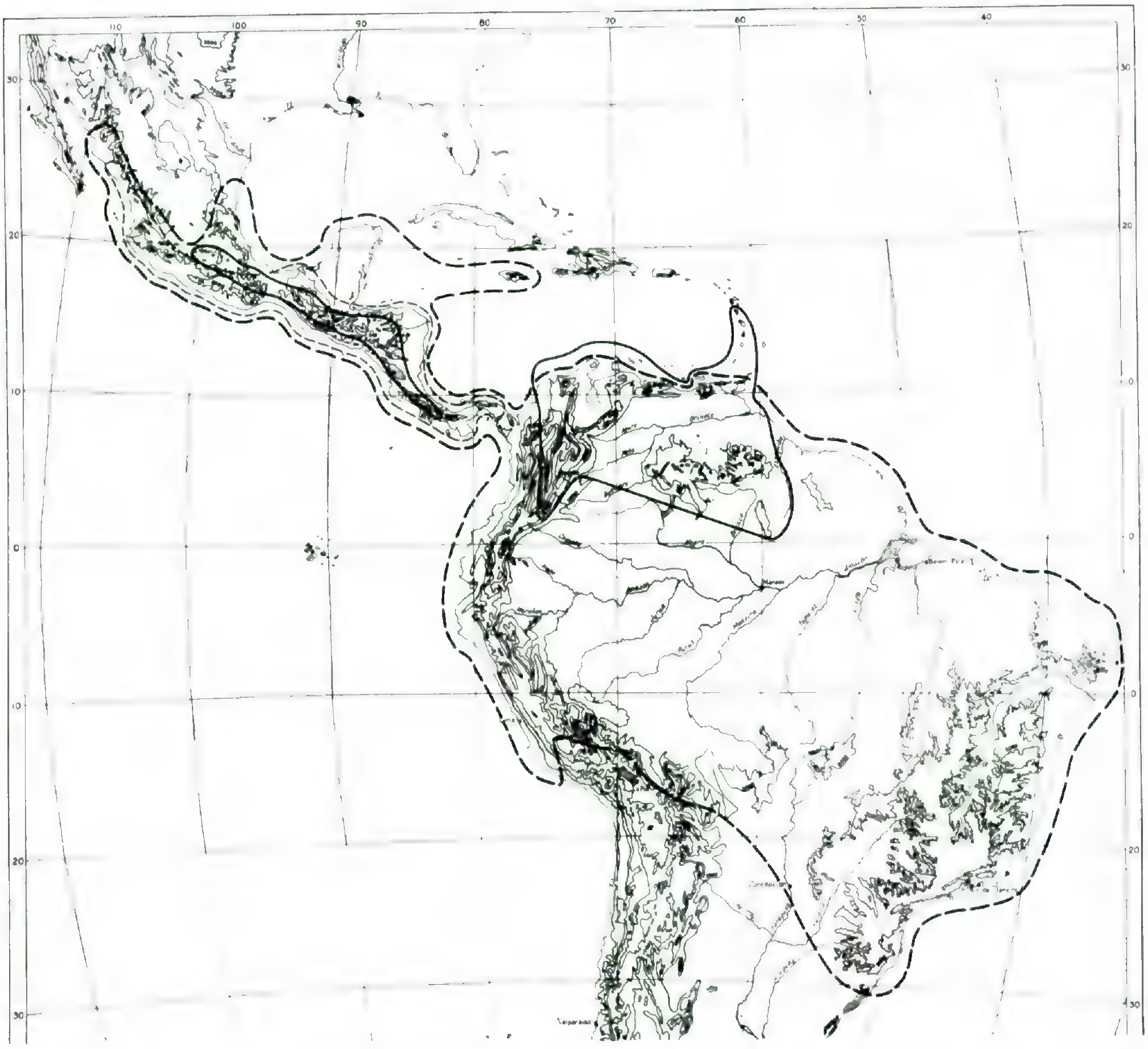


FIGURE 7. Distribution of the species of *Glossophaga*: *soricina* (bold dashed line), *commissarisi* (fine dashed line in Middle America), *alticola* (solid line in Middle America), *longirostris* (solid line in South America).

nectar feeders also eat small insects, many of which can be obtained in and around flowers. In these, there is some retention of molar cusps which are used for chewing up insects (Phillips, 1971) and of stomachs which still resemble those (Forman et al., 1979) of primitive insectivorous bats to a considerable degree. In more highly specialized nectar-feeders, pollen largely replaces insects as a significant protein source, and Howell (1974) has presented evidence that at least one such highly specialized nectar-feeder (*Leptonycteris sanborni*) obtains pollen with a richer protein content from the flowers which it pollinates than those which are normally pollinated by insects. These more highly derived nectar-feeders have teeth and stomachs which reflect the virtually total dependence of these bats on flowers for both carbohydrate and protein. The dependence is, of course, mutual since a number of flowering plants have special adaptations for pollination by bats.

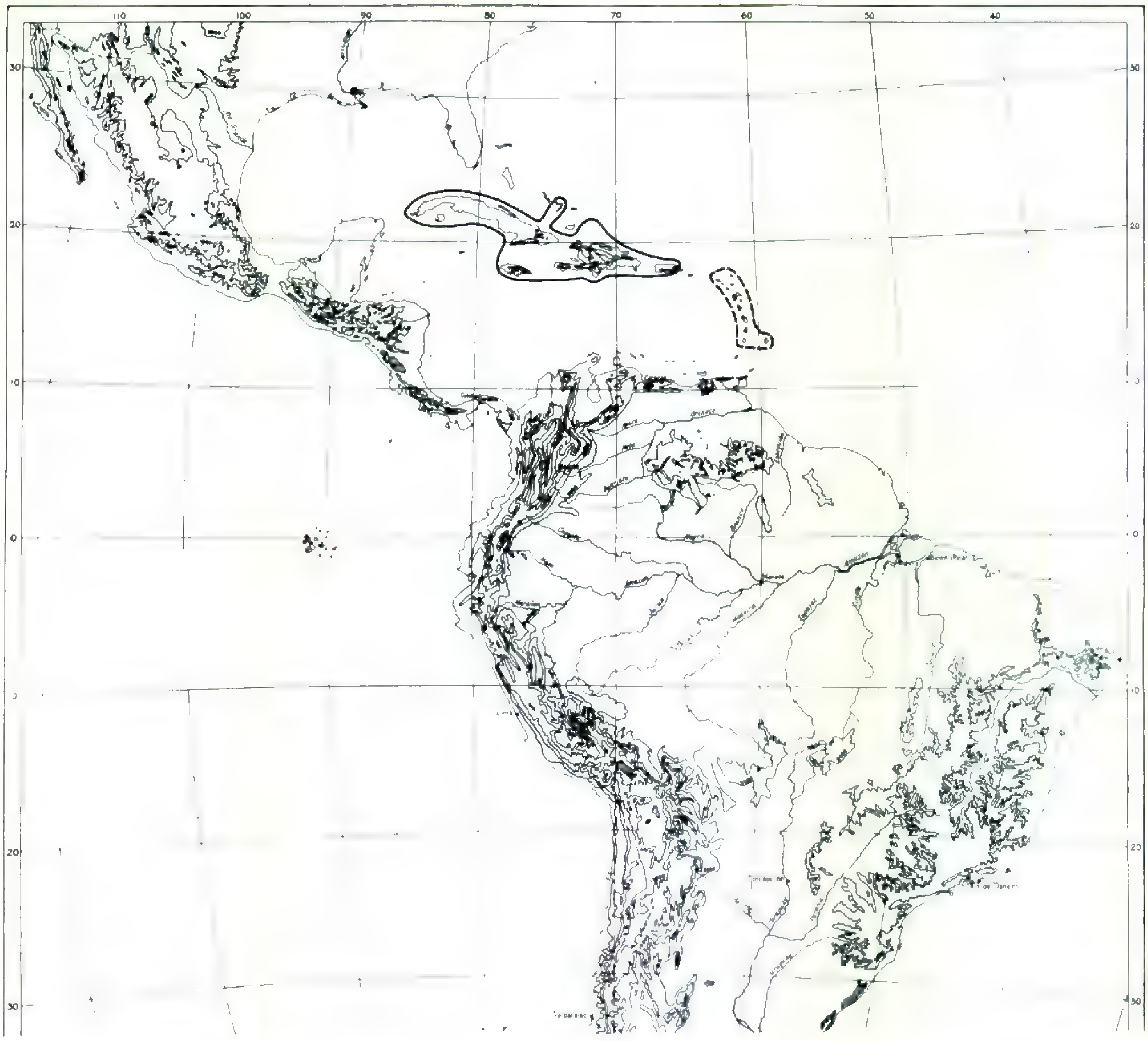


FIGURE 8. Distribution of the species of *Monophyllus*: *redmani* (solid line), *plethodon* (dashed line).

DISTRIBUTION OF NEW WORLD NECTAR-FEEDING BATS

The nectar-feeding bats of the New World are all referable to the family Phyllostomidae, which, as we have already seen, is extraordinarily diverse in both morphology and food habits. Two subfamilies are currently recognized to include the nectar-feeders. The Glossophaginae, containing 13 currently recognized genera have a wide distribution in the tropics and subtropics of North and South America as well as the West Indies. The Brachyphyllinae include three genera confined to the West Indies which possibly had a different origin within the family from that of the Glossophaginae. One of its genera (*Brachyphylla*) was until recently classified as a member of the fruit-eating subfamily Stenodermatinae since its teeth are heavier than those of other nectar-feeders (Fig. 4). While it is known to feed on nectar and pollen (Silva Taboada & Pine, 1969), it does not seem to be a specialist but is at least in part a fruit-eater. Other characters,

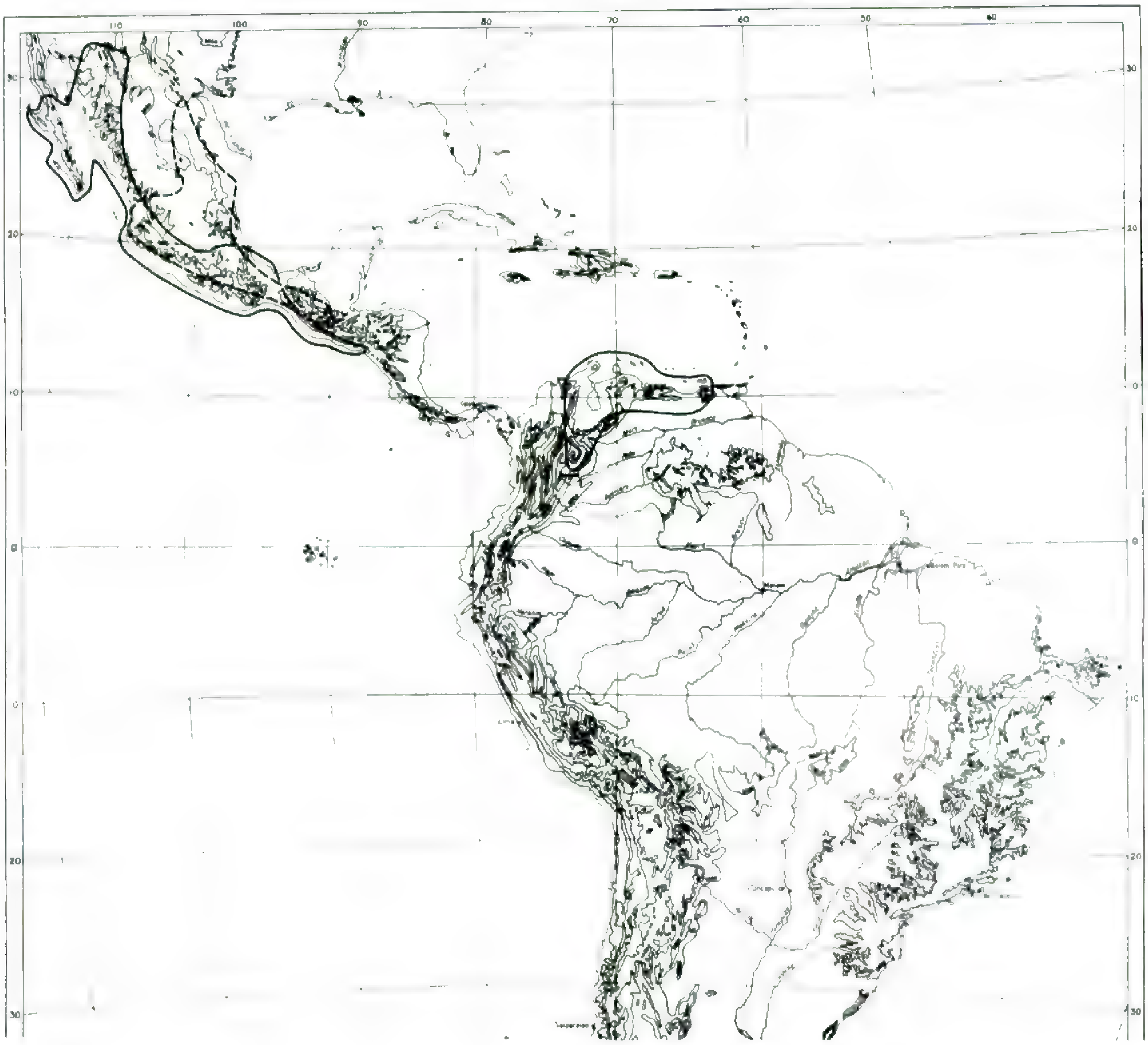


FIGURE 9. Distribution of the species of *Leptonycteris*: *sanborni* (solid line in Middle America), *nivalis* (dashed line), *curasoae* (solid line in South America).

however, seem to ally it with the other two genera included in the subfamily Brachyphyllinae.

DISTRIBUTION OF THE GLOSSOPHAGINE

There is a great deal of disagreement concerning relationships within this subfamily, but I will use the order of genera employed by Jones & Carter (1976). It should be pointed out that several authors have regarded the glossophagines as polyphyletic. However, they disagree among themselves concerning the proper allocation of various genera to the separate clades.

Genus Glossophaga (Fig. 7).—This is a primitive genus with four currently recognized species. The commonest and most widespread, *G. soricina*, has an extensive distribution in Middle and tropical South America. It also reaches Jamaica and has been recorded from the Bahamas. Two other species, *alticola* and *commissarisi*, are known only from Middle America, though the latter is suspected to occur in northwestern South America. The fourth species, *longirostris*,

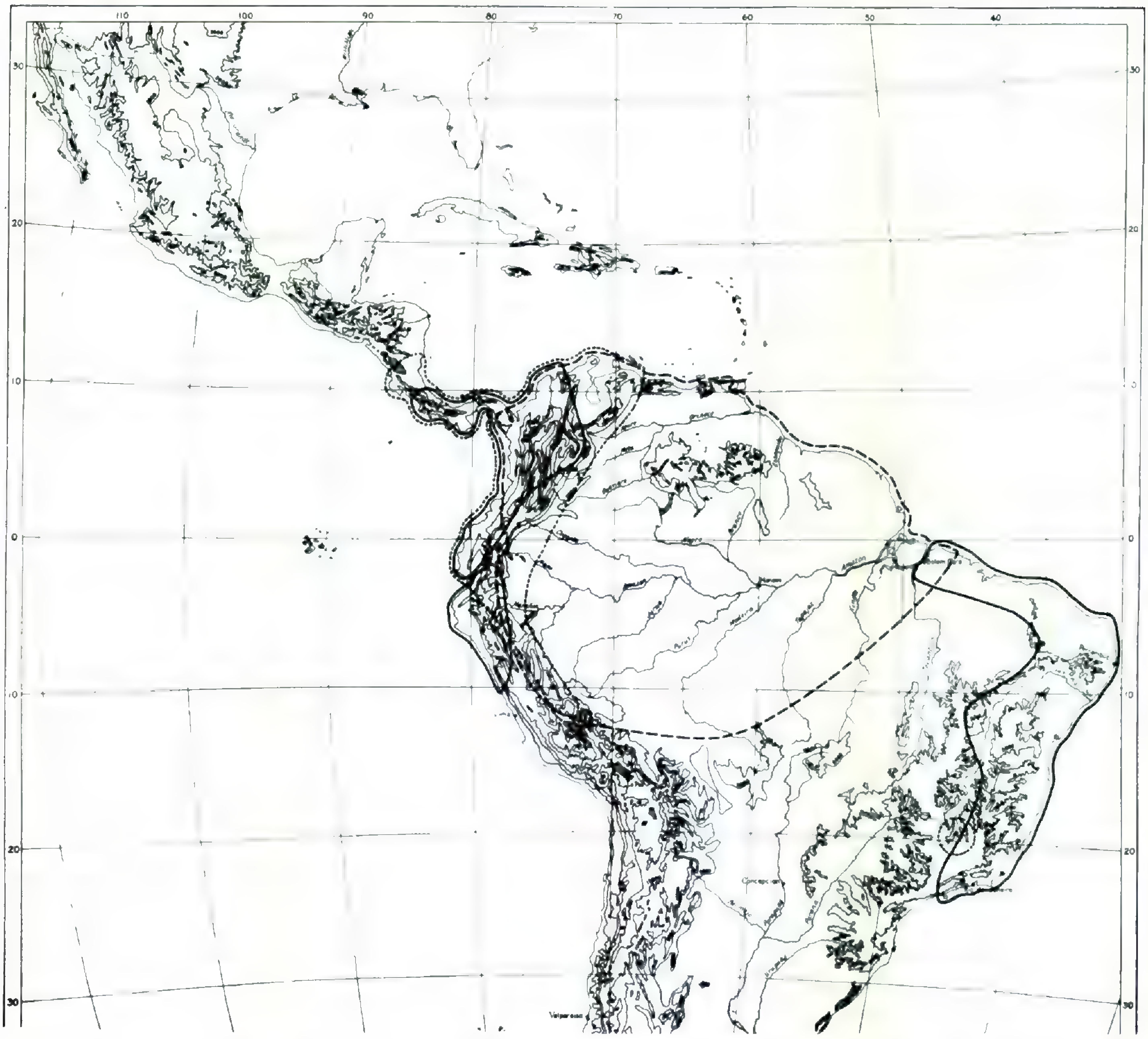


FIGURE 10. Distribution of the species of *Lonchophylla*: *thomasi* (dashed line), *mordax* (solid lines in Central and northwestern South America and in eastern Brazil), *robusta* (dotted line in Central and northwestern South America), *bokermanni* (dotted line in southeastern Brazil), *hesperia* (solid line in Peru).

occurs in northern South America but also reaches several islands off the coast including the southern Lesser Antilles.

Genus Monophyllus (Fig. 8).—This genus is closely related to *Glossophaga*, particularly to *G. longirostris*. The genus is confined to the West Indies and consists of two species. *Monophyllus redmani* is found in the Greater Antilles and southern Bahamas, whereas *M. plethodon* is at present confined to the Lesser Antilles, though it is known as a fossil from Puerto Rico (along with *M. redmani*).

Genus Leptonycteris (Fig. 9).—This is a fairly derived genus about which more is known of food habits (particularly pollen) than any other. It is probably better adapted to semiarid conditions than most other New World nectar-feeders. As a result, its distribution actually seems to avoid the wet tropics favored by most phyllostomid bats. Two of the species, *sanborni* (=*yerbabuenae*) and *nivalis*, range from the southwestern United States to northern Central America, though they are only summer residents in the northern ends of their ranges. The

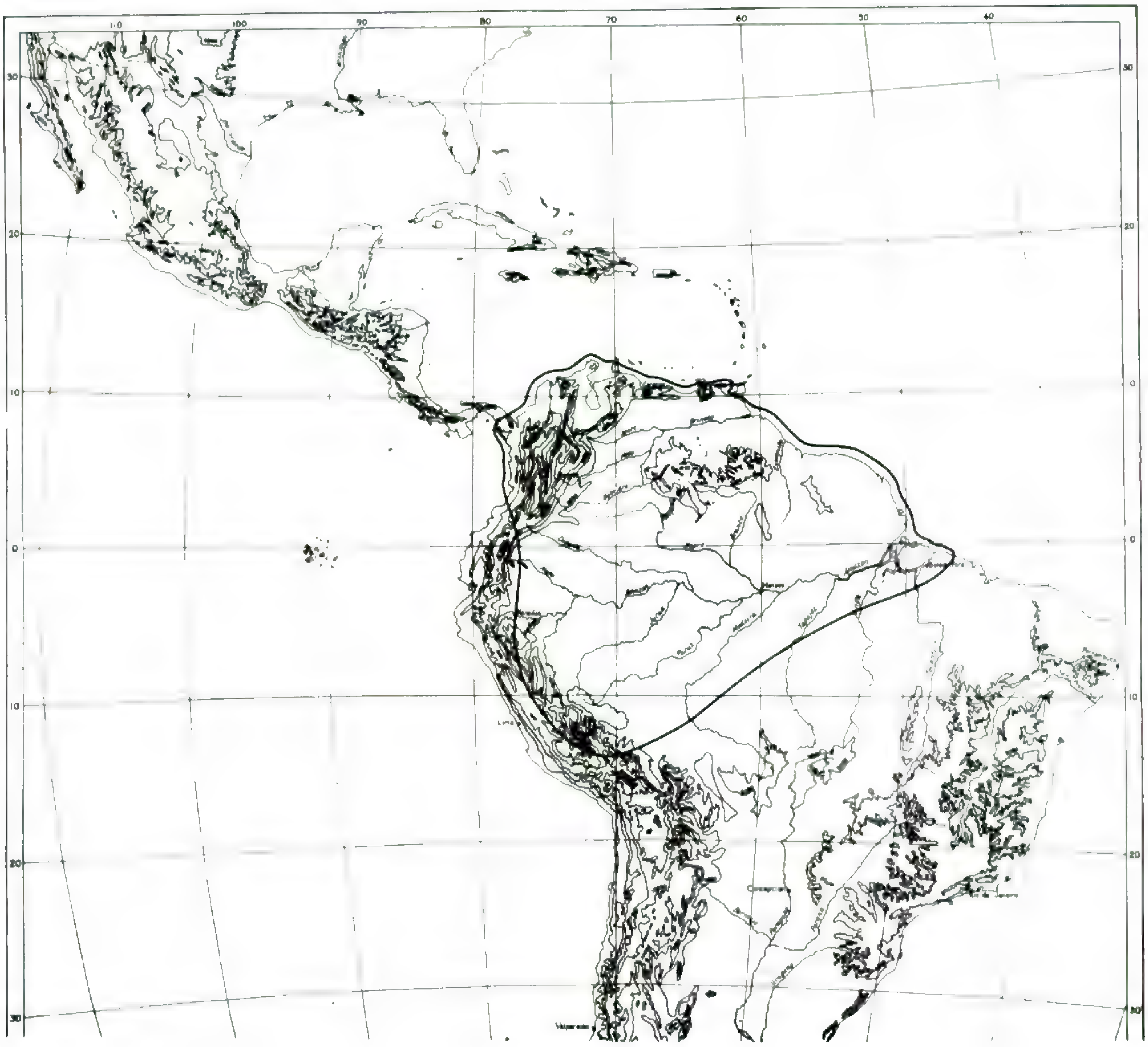


FIGURE 11. Distribution of *Lionycteris spurrelli* (solid line).

third, *curasoae*, is confined to extreme northern South America and reaches several offshore islands.

Genus Lonchophylla (Fig. 10).—Five species may be recognized in this fairly primitive genus. *Lonchophylla thomasi* has basically an Amazonian distribution but reaches Panama. *Lonchophylla mordax* (including *concava*) ranges from Costa Rica to Ecuador and also occurs in eastern Brazil, the two discontinuous portions of the range often being considered two species. *Lonchophylla robusta* ranges from Nicaragua through lower Central America and northwestern South America to Peru. The recently described *bokermanni* (Sazima et al., 1978) is known only from a small area in southeastern Brazil. Finally, *L. hesperia* is known only from a relatively arid area in southwestern Ecuador and northwestern Peru.

Genus Lionycteris (Fig. 11).—The single species, *spurrelli*, of this primitive genus is basically Amazonian but reaches Panama.

Genus Anoura (Fig. 12).—This fairly primitive genus probably contains only three species (Nagorsen & Tamsitt, 1981). *Anoura caudifer* is confined to

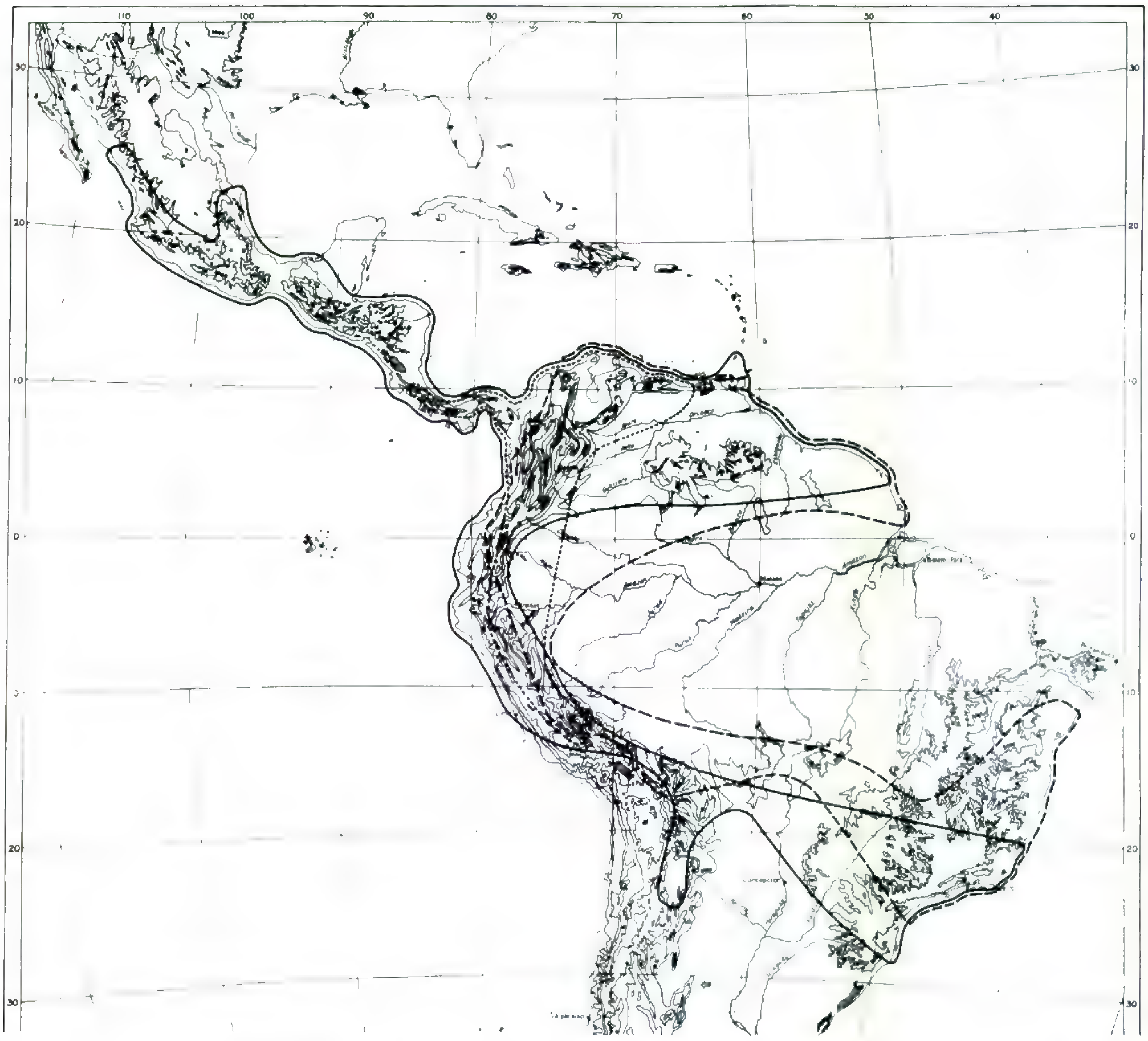


FIGURE 12. Distribution of the species of *Anoura*: *caudifer* (dashed line), *cultrata* (dotted line), *geoffroyi* (solid line).

tropical South America where it is fairly widespread but seems to avoid most of the Amazon basin. *Anoura cultrata* (including *brevirostrum* and *werckleae*, Nagorsen & Tamsitt, 1981) occurs in lower Central America and northwestern South America from Costa Rica to Peru. *Anoura geoffroyi*, like *caudifer*, is widespread in tropical South America, yet avoids most of the Amazon basin; it also extends north to tropical Mexico and onto a few off-shore islands.

Genus Scleronycteris (Fig. 13).—This highly derived genus is known by a single poorly known species, *S. ega*. The two known localities are both in the Amazon basin.

Genus Lichonycteris (Fig. 13).—This highly derived genus has two poorly defined species. *Lichonycteris obscura* ranges from Guatemala to Peru and Suriname but largely outside the Amazon basin. The few known localities for *L. degener* are all within the Amazon-Orinoco basin.

Genus Hylonycteris (Fig. 13).—This highly derived genus has a single species, *H. underwoodi*, confined to Middle America (southern Mexico to Panama).

FIGURE 13. Distribution of the species of *Scleronycteris*, *Lichonycteris*, *Hylonycteris*, and *Platalina*: *S. ega* (dotted line), *L. obscura* (solid line in Central and northwestern South America), *L. degener* (solid line in Amazon basin), *H. underwoodi* (dashed line in Middle America), *genovensium* (dashed line in Peru).

Genus Platalina (Fig. 13).—This is another highly derived genus with one species (*P. genovensium*), confined in this case to the arid coast (and some interior valleys) of Peru. It is particularly noteworthy for its very long rostrum (and presumably extra long tongue).

Genus Choeroniscus (Fig. 14).—There are four species of this highly derived genus. *Choeroniscus godmani* occurs in Middle America and northern South America (western Mexico to Guyana). *Choeroniscus minor* (including *inca*, see Koopman, 1978) is confined to northern South America and so is the closely related *C. intermedia*. *Choeroniscus periosus* is confined to a small area in the very wet forest of western Colombia.

Genus Choeronycteris (Fig. 15).—This highly derived genus has a single species, *C. mexicana*, ranging from the southwestern United States to Honduras but only as a summer resident at the northern end of its range. Though a subspecies (*ponsi*) has been described from Venezuela, it is doubtful that it belongs

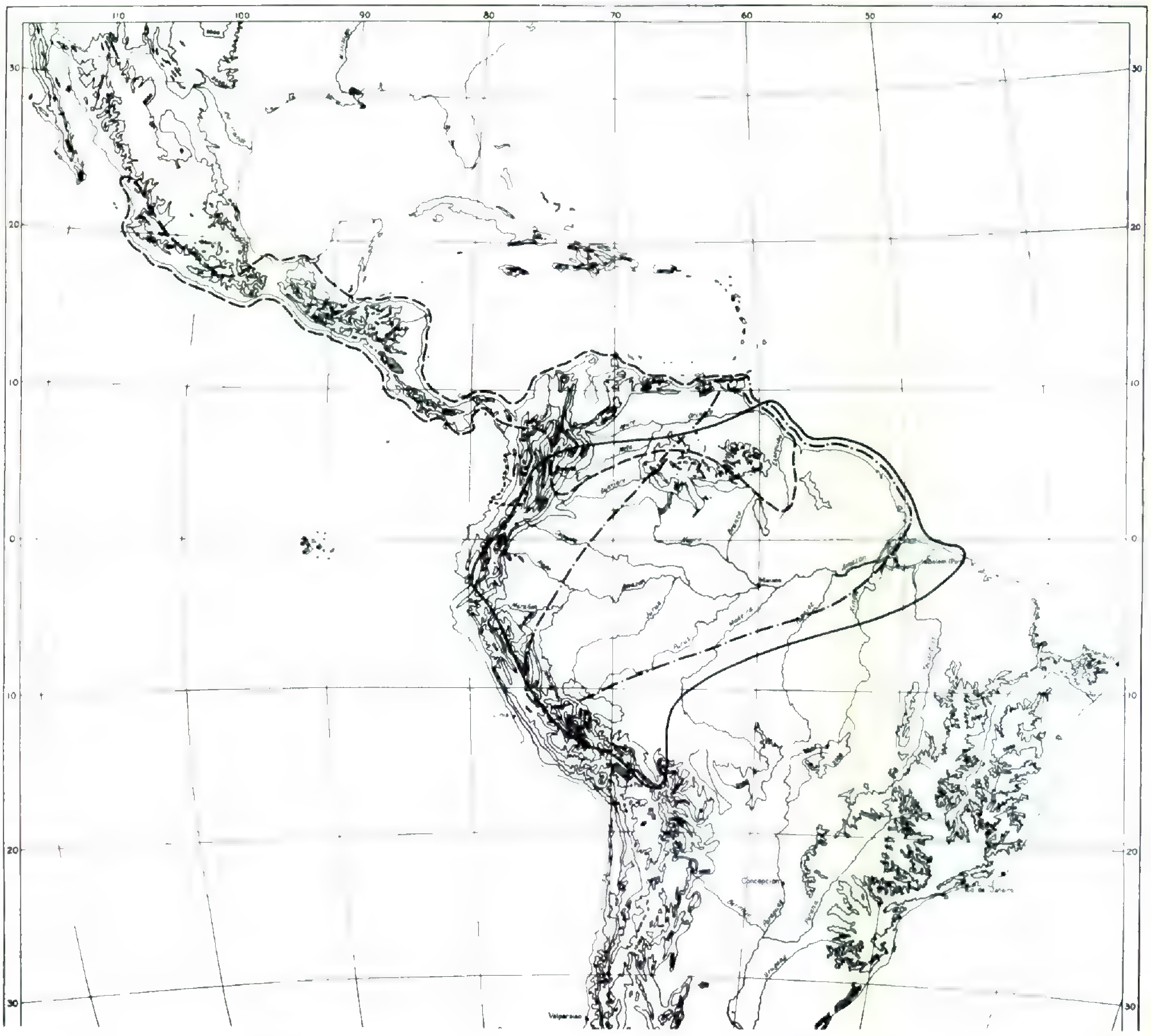


FIGURE 14. Distribution of the species of *Choeroniscus*: *godmani* (dashed line in Middle and northern South America), *intermedius* (dotted and dashed line), *minor* (solid line), *periosus* (dotted line in western Colombia).

to the Middle American species (see Jones & Carter, 1976). Like *Platalina*, *Choeronycteris* has an unusually long rostrum which almost certainly indicates a very long tongue.

Genus Musonycteris (Fig. 15).—This genus is closely related to *Choeronycteris* (with which it has been united by some) but has a still longer rostrum, in fact the longest (in relation to its width) of any bat (Fig. 1). The single species, *M. harrisoni*, is confined to southwestern Mexico.

DISTRIBUTION OF THE BRACHYPHYLLINAE

Unlike the subfamily Glossophaginae, that of the Brachyphyllinae is confined to the West Indies. Two of the three currently recognized genera (*Erophylla* and *Phyllonycteris*) have the skull and tongue proportions of typical nectar feeders, but the third, *Brachyphylla* has a head and dentition (Fig. 4) built like that of a fruit-eater. For this reason, it was for many years placed in the fruit-eating

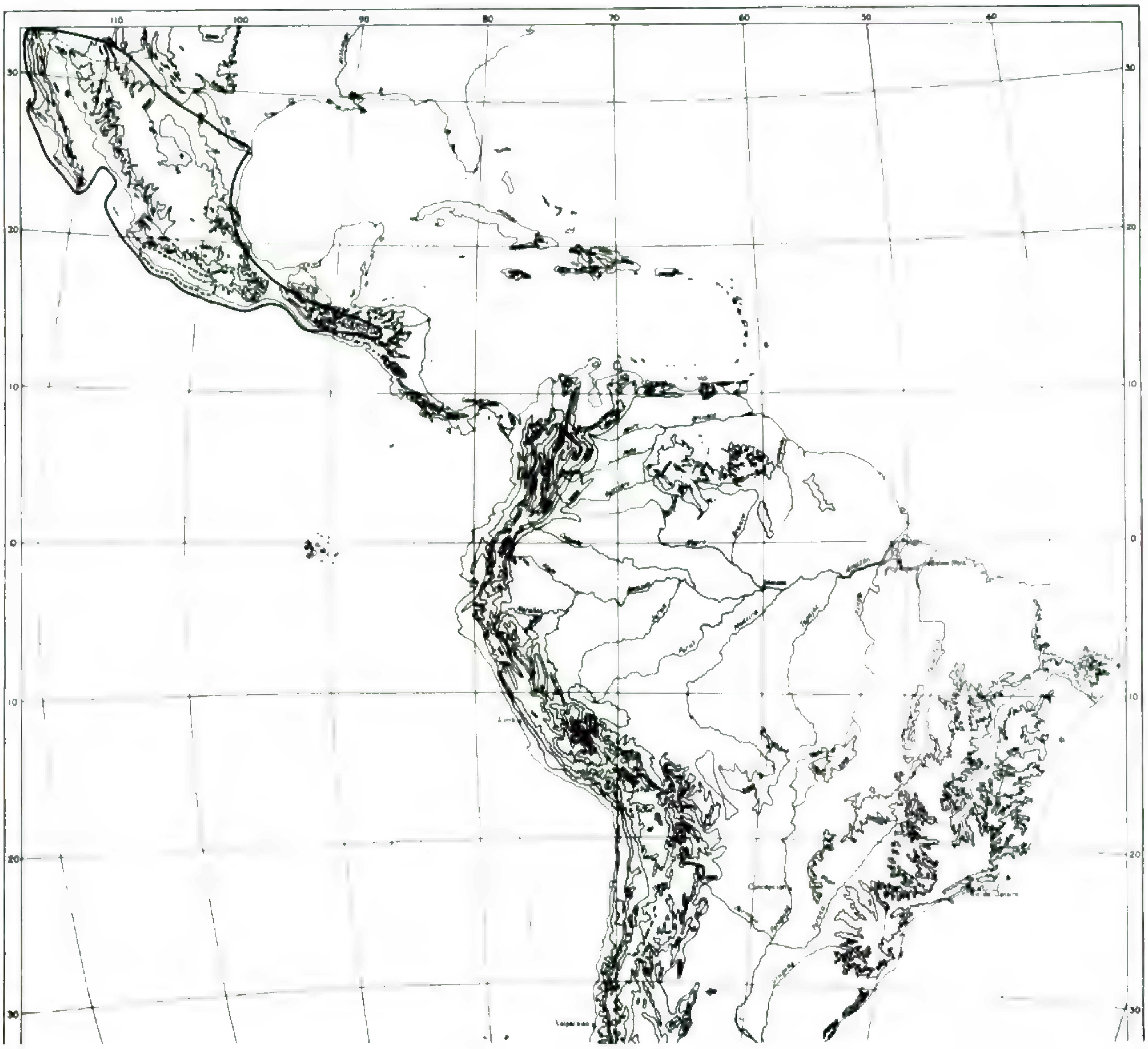


FIGURE 15. Distribution of the species of *Choeronycteris* and *Musonycteris*: *C. mexicana* (solid line), *M. harrisoni* (dotted line).

subfamily Stenodermatinae. What little is known of its food habits indicates a mixture of fruit and nectar. The other two brachyphylline genera also eat soft fruit on occasion.

Genus Brachyphylla (Fig. 16).—Two species are currently recognized, *nana* in Cuba, Hispaniola, the southern Bahamas, Cayman Islands (and known fossil from Jamaica); *cavernarum* in Puerto Rico and the Lesser Antilles.

Genus Erophylla (Fig. 16).—Again two species are recognized, *sezekorni* in Cuba, Jamaica, the Cayman Islands, and the Bahamas; *bombifrons* in Hispaniola and Puerto Rico.

Genus Phyllonycteris (Fig. 16).—This, like *Erophylla*, is a very highly specialized nectar-feeding bat. There are two living species, *poeyi* in Cuba and Hispaniola, *aphylla* in Jamaica. A third species, *major*, is known as a fossil from Puerto Rico.

ORIGIN AND DIVERSIFICATION OF NEW WORLD NECTAR-FEEDING BATS

The Phyllostomidae, the family to which all New World nectar-feeding bats belong, probably originated in tropical America since not only this family but the

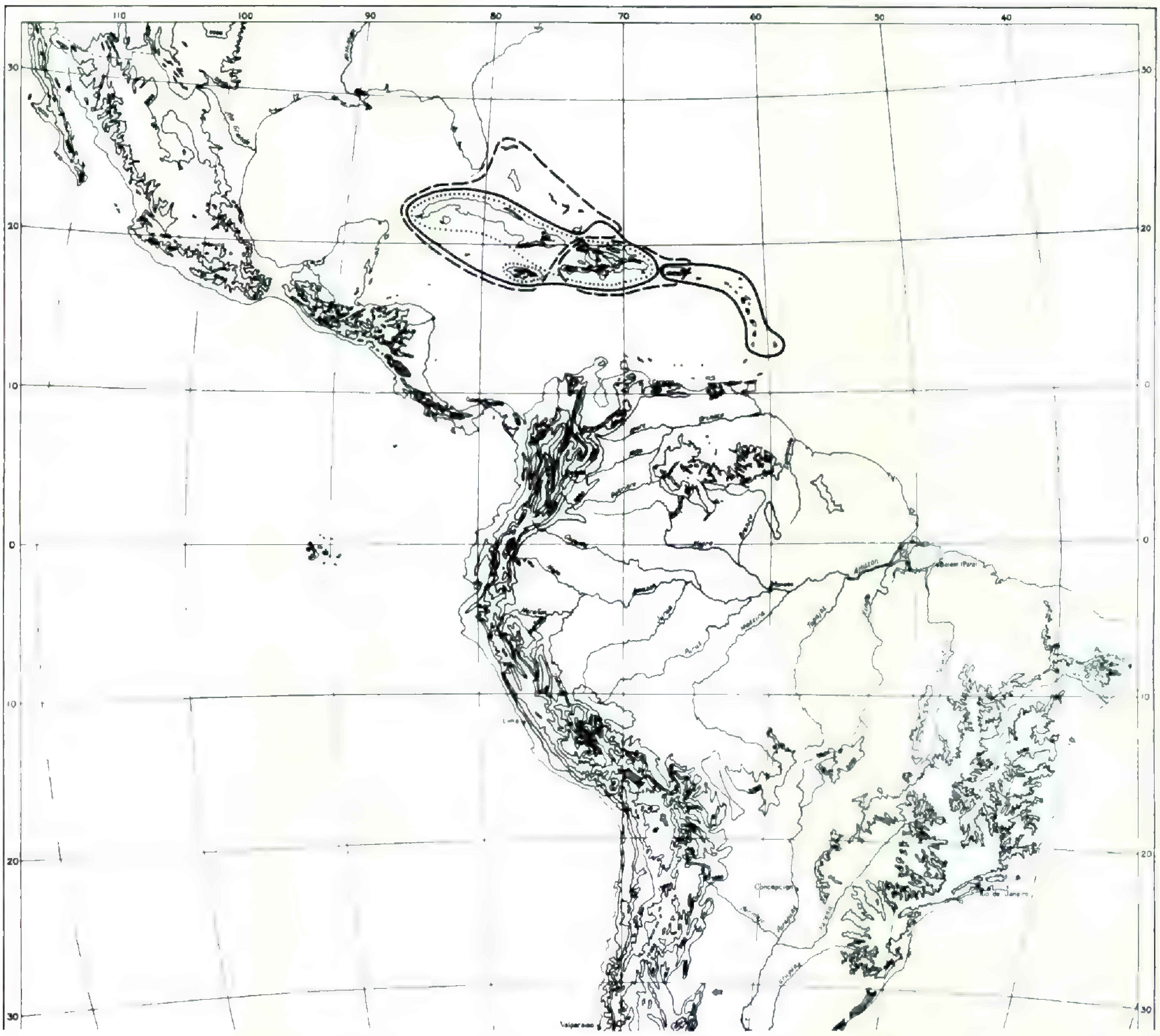


FIGURE 16. Distribution of the species of the Brachyphyllinae: ***Brachyphylla nana*** (solid line in the Greater Antilles), ***B. cavernarum*** (solid line in Puerto Rico and the Lesser Antilles), ***Erophylla sezekorni*** (dashed line in the Bahamas and western Greater Antilles), ***E. bombifrons*** (dashed line in the eastern Greater Antilles), ***Phyllonycteris poeyi*** (dotted line in Cuba and Hispaniola), ***P. aphylla*** (dotted line in Jamaica).

two most closely related families (Noctilionidae and Mormoopidae) are largely confined to this region. The earliest known fossil phyllostomid (not a glossophagine) is from the late Miocene of Colombia. At this time South America was still an island continent, separated by a marine channel from Central America, which suggests that the family originated in South America in long isolation. Unfortunately, the fossil record of bats in general and phyllostomids in particular is so poor that this can only be a suggestion. It is also highly uncertain when nectar-feeding bats evolved since none are known as fossils before the Pleistocene, but probably this occurred sometime during the middle or later Cenozoic. If both of these conclusions are valid, then the subfamily Glossophagine probably also arose in South America, but if so there has been extensive secondary spread to Middle America. Of the 12 mainland genera here recognized, only two (*Scleronycteris* and *Platalina*) are confined to South America, whereas three (*Hylonycteris, Choeronycteris, Musonycteris*) are confined to Middle America (including extreme southwestern North America). Of the remaining seven genera, three

have extensive South American but restricted Middle American distributions (*Lionycteris* to Panama, *Lonchophylla* to Nicaragua, *Lichonycteris* to Guatemala). *Glossophaga, Anoura,* and *Choeroniscus* all have extensive distributions in both South and Middle America. *Leptonycteris* has a peculiar distribution, southwestern North America to upper Central America, also extreme northern South America, but with an apparently real hiatus in between. As suggested above, this may reflect a preference for relatively dry areas. Other glossophagine genera, however, with apparently similar ecological preferences (*Platalina, Choeronycteris, Musonycteris*) do not show the same distributional pattern.

The Colonization of the West Indies

The West Indian nectar-feeders belong to two distinct groups. *Glossophaga* and *Monophyllus* are typical (and quite primitive) glossophagines whereas *Erophylla* and *Phyllonycteris,* together with the somewhat differently adapted *Brachyphylla,* form the highly derived endemic West Indian subfamily Brachyphyllinae. There is considerable disagreement concerning the relationships of the Brachyphyllinae. Thomas Griffiths at the University of Massachusetts is currently investigating relationships among all the New World nectar-feeding bats, and hopefully he will resolve the problem of the origin of the Brachyphyllinae. Currently, he is inclined to derive them from the base of the Glossophagine (Griffiths, oral communication). What can be said with confidence at this time is that the brachyphyllines have almost certainly been in the West Indies for a long time, probably since the Miocene, since this is the best differentiated group of endemic Antillean bats. *Monophyllus* is a much more recent invader (probably from South American *Glossophaga longirostris*), and still more recently, two different species of *Glossophaga* have colonized limited areas at the opposite ends of the West Indian chain.

Ecological Interactions of the New World Nectar-feeding Bats

In view of the mutual adaptations of flower-feeding bats and the flowers with which they are associated, it would be very interesting if we could correlate their distributions and associate particular flower-feeders with the angiosperms which they pollinate. Unfortunately, not enough is known about the particular flowers visited by particular bat species to make any useful correlations. Skog (1976) has shown that head size of Greater Antillean nectar-feeding bats can be correlated with corolla size of species of *Gesneria* (which have adaptations for bat pollination) occurring on the same islands. Unfortunately, it is not known whether or not these particular species of bats do pollinate these particular species of *Gesneria.* Experience with predicting food habits on the basis of jaw and tooth characteristics in bats shows that correlations are usually far from perfect and sometimes quite poor.

Another factor that must be taken into account is that since none of the nectar-feeding bats hibernates and since all bats have surprisingly long life spans (more than 10 years), it is necessary for them to find flowers all year round. While there is apparently considerable irregular wandering (albeit undocumented) and, as we have seen, some definite migrations of north-temperate species, they still have

to find flowers blooming somewhere throughout the year. Since a given species of angiosperm is usually in flower for a limited time, a bat species dependent upon flowers must make repeated shifts. Rigid specialization for a certain type of flower is therefore unlikely, and an unusually long rostrum and tongue need not imply that only flowers with long corollas are visited. This may only mean that during one part (perhaps a very short part) of the year, this bat depends for food on nectar or pollen, which can only be reached with a very long tongue.

Nevertheless, when two or more species of nectar-feeding bats occur in the same area at the same time, one would expect some niche-partitioning of the flowers visited, assuming of course that some other necessary resource (such as roosting sites) was not in shorter supply. So far, direct evidence of this is virtually nonexistent. I have already mentioned various nectar-feeders which seem to be restricted to arid regions (*Leptonycteris, Lonchophylla hesperia, Platalina, Choeronycteris, Musonycteris*). However, most flower-feeding bats occur in the wet tropics. As indicated above, the most distinctive geographical separation is between mainland and West Indian species. There is also a weak separation on the mainland between South and Middle American species. I have checked wet tropical areas where collections have been extensive and where more than three species of nectar feeders (excluding the arid-adapted ones) are known to occur. I have come up with 10 such limited areas which merit some discussion.

Cuba. This large West Indian island has four of the species under discussion (*Monophyllus redmani, Brachyphylla nana, Erophylla sezekorni, Phyllonycteris poeyi*). As mentioned above, *Brachyphylla* is only partially a nectar-feeder. Judging by molar tooth patterns, *Monophyllus* has somewhat different adaptations from *Erophylla* and *Phyllonycteris*.

Hispaniola. The same species occur as in Cuba, except that *Erophylla bombifrons* replaces *E. sezekorni*.

Jamaica. This West Indian island also has four nectar-feeding bats (*Glossophaga soricina, Monophyllus redmani, Erophylla sezekorni, Phyllonycteris aphylla.*) *Glossophaga* and *Monophyllus* are at least dentally much more primitive than *Erophylla* and *Phyllonycteris*.

Sinaloa. This western Mexican state lies near the northern end of the tropics. There are four wet-tropical glossophagines (*Glossophaga soricina, G. commissarisi, Anoura geoffroyi, Choeroniscus godmani*). Though there is some adaptive spread among these species, it is not clear how they partition the habitats).

Oaxaca. This is another western Mexican state, but one less marginal to the tropics. There are six species of the sort under consideration (*Glossophaga soricina, G. commissarisi, G. alticola, Anoura geoffroyi, Hylonycteris underwoodi, Choeroniscus godmani*). Though the first three are certainly more primitive than the last three, it is not clear how this relates to niche partitioning.

Eastern Panama. This area, at the junction of South and Middle America, has seven relevant species (*Glossophaga soricina, G. commissarisi, Lonchophylla thomasi, T. mordax, T. robusta, Lionycteris spurrelli, Lichonycteris obscura*). Again, there is a fair adaptive spread, but little evidence for niche partitioning.

Mérida region. This well-collected area in western Venezuela has six species of nectar-feeders (*Glossophaga soricina, G. longirostris, Lonchophylla robusta, Anoura caudifer, A. cultrata, A. geoffroyi*). In view of its location near the north-

ern end of the Andes, some altitudinal stratification might be supposed. However, all six species occur in the lowlands and all but *G. longirostris* also in the highlands (above 1000 m).

Trinidad. This well-collected continental island off the northern coast of South America has four species of glossophagine bats (*Glossophaga soricina, G. longirostris, Anoura geoffroyi, Choeroniscus intermedius*). Though both primitive and derived species are represented, I know of no evidence of niche-partitioning on the basis of food.

Belém region. This well-collected area near the mouth of the Amazon is different from any of the others here treated in that it is completely lowland, without any mountains nearby. Six species of glossophagines occur (*Glossophaga soricina, Lonchophylla thomasi, L. mordax, Lionycteris spurrelli, Lichonycteris degener, Choeroniscus minor*). Again, there is considerable diversity in degrees and types of specialization, but no evidence of niche partitioning.

Amazonian slopes of central Peru. Another well-collected area in the tropical heart of South America; 10 species of glossophagines are known (*Glossophaga soricina, Lonchophylla thomasi, L. robusta, Lionycteris spurrelli, Anoura caudifer, A. cultrata, A. geoffroyi, Lichonycteris obscura, Choeroniscus minor, C. intermedia*. Although there is considerable evidence concerning altitudinal ranges in this area (see Koopman, 1978), this does little to explain niche partitioning among the glossophagines. All species occur in the lowlands and half of the species (those in *Glossophaga, Lionycteris,* and *Anoura*) reach the highlands, though the *Anoura* species reach much higher elevations than either *Glossophaga* or *Lionycteris*.

Thus, summing up this information concerning species in local areas, there is little evidence among species inhabiting the wet topics for any niche partitioning either on the basis of kinds of flowers visited or altitudes at which foraging occurs. Of course, since a bat's roosting site and its foraging range may be well separated, it is possible that there is more separation in actual places where flowers are visited than the total range would indicate. Though, on the evidence of considerable morphological diversity, I would expect some niche partitioning based on food plants, there is very little evidence of any at this time.

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Note added in proof: Since this paper was submitted, two additional species of Glossophaginae have been described. *Glossophaga mexicana* (Webster & Jones, 1980. Occ. Papers Texas Tech. Univ. 71: 1–12) is from southwestern Mexico. *Lonchophylla handleyi* (Hill, 1980. Bull. Br. Mus. Nat. Hist., Zool. 38: 233) has been split off from *L. robusta,* which does not occur south of Ecuador. *Lonchophylla handleyi* is in Ecuador and Peru.

THE ENERGETICS OF POLLINATION

BERND HEINRICH[1]

Many animals derive their food energy from the nectar of flowers, and the flowers may also provide them with the materials for growth and reproduction. To the plants, in turn, the animals are the vehicle for the transport of male gametes for fertilization. As a consequence, there is a mutual interdependence involving a set of evolved "games" where the pollinators try to get the most for their foraging effort, while flowers provide the least reward possible. The flowers must provide enough reward to attract the pollinators and keep them from visiting competitor species, but the rewards must be sufficiently small to keep them moving from one plant to another (Heinrich & Raven, 1972). Interesting complications arise in this simple scheme in male vs. female functions of flowers, when many-flowered vs. few- or single-flowered plants are considered, and when any one plant's most potent competitors are other individuals of the same rather than other species. The latter aspects have been little explored.

In order for the pollination system to "work" requires several conditions. First, there must be advertisement of the rewards. Secondly, flower morphology must be appropriate for the pollinator to become dusted with pollen without dusting the pistil, and to transfer this pollen to a receptive pistil of another flower. The morphological features of the flower act to manipulate the close-in behavior of the pollinator to increase the percentage of cross-pollination events per given food reward provided, or per given forager-flower encounter (Macior, 1974). It is probably a safe working hypothesis that the foragers have selected, by those visits that have resulted in fertilization, most of the flowers that we know today. They have been the agents of flower horticulture in nature, and if we want to observe the selective pressures that have shaped or are shaping flower evolution, we must look to the foraging behavior of the flower visitors.

The third major consideration is that the foragers must not only be appropriately manipulated at the flowers, they must also be caused to move between them (Heinrich & Raven, 1972). This involves energetics. And when one looks from the standpoint of energetics, it becomes necessary to consider the environment and the other plants relative to whom the pollinator's choices are made.

Most pollinators are inherently promiscuous; they visit flowers for the rewards they contain, regardless of the shape or color of the flower's exterior. But to the plant, to whom flower constancy is important for cross-pollination, fidelity can be "bought" by providing large food rewards. But this purchase may be at a high price. In the immediate, ecological, sense, too strict a fidelity will hinder the contribution of male gametes to other flowers. A bee, for example, will return repeatedly to a single blossom, visiting no others, provided this blossom is sufficiently rewarding, conspicuous and isolated (McGregor et al., 1959). A second cost, one that may not be apparent unless measured against an evolutionary time

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span, is that calories used to feed pollinators are no longer available to be thrown into fruit and seed production.

The energetics of pollination is now an old topic. It is at least eight years old. In the last several years, a flood of excellent research has been published. The foraging behavior of many kinds of nectivores has been explored (Heithaus et al., 1974; Heinrich, 1979a, 1979b; Howell, 1979). Ecological studies have examined the important role of the pollinator's competition for food resources in shaping various plant communities (Moldenke, 1975; Inouye, 1978; Ostler & Harper, 1978; Schemske et al., 1978; Moral & Standley, 1979). Many studies on the foraging behavior in the field in various parts of the world have been aimed, in part, to gain insights into ecology and evolution (Macior, 1974; Willson & Rathke, 1974; Stiles, 1975; Carpenter, 1976; Frankie et al., 1976; Regal, 1977; Feinsinger, 1978; Silander & Primack, 1978; Sussman & Raven, 1978; Waser, 1978a, 1978b; Ford, 1979). It is not possible for me here to more than briefly mention a very small portion of the work that has been done. My aim will be to provide several contrasting examples illustrating different concepts, and to point out what these suggest in regard to new and productive research.

Interspecific Competition and Flowering Divergence

An implicit early assumption in pollination energetics was that the energy balance between pollinators and the food rewards of flowers, which provides the selective pressure both to improve foraging efficiency and flower evolution, was competition. There is now a general concensus in the majority of recent papers on the theme of energy balance in pollination ecology that plants compete for pollinators, and that pollinators compete for plants. However, what is not always distinguished is whether one is dealing with the ecological or evolutionary time scales. Also, it must be recognized that perhaps in the ecological context and particularly in the evolutionary context, both competition for and between pollinators may be occurring simultaneously; all of the pollinators may be competing for the nectar provided by the highest nectar producers, while the lowest nectar producers may remain unpollinated. Relatively few papers have so far been addressed to intraspecific competition and the energy investment of plants in this competition to total flowering as well as to nectar production (but see Willson & Rathke, 1974; Silander & Primack, 1978; Schaeffer & Schaeffer, 1979).

Competition between pollinators is inferred from the fact that nectar is a highly-prized resource that is generally removed from flowers, by any of a variety of pollinators, soon after it becomes available. Secondly, the numerous intricate behaviors and specialized morphologies of nectivores that have evolved for foraging suggest that these animals have been under long selective pressure to perfect their foraging techniques. If pollinator populations are limited by food supplies, then they should increase until all the available resources are utilized, and the different kinds of flowers are each visited in proportion to the food rewards available from them. Until the pollinators reach saturation densities, the most highly rewarding species may thus receive adequate pollination service, while the remainder, with relatively less net food rewards, may remain unpollinated, unless they shift their blooming to a less crowded time. "Cornucopian species" such as *Salix* spp. and *Taraxacum officionale*, for example, may disproportionately at-

tract insects, causing these pollinators to abandon other spring flowers (Mosquin, 1971). Similar competition between species in the natural habitat is one proposed mechanism for the evolution of sequential blooming. Waser (1978a, 1978b) has recently pointed out, however, that "because a preferred species suffers no reproductive loss when flowering with a less attractive species, it should lengthen its flowering period in the absence of other constraints until it has completely excluded the less attractive species from the community or completely overlaps with it in flowering time." He proposes, instead, that a second, probably more ubiquitous, mechanism of competition for pollination involves loss of viability from interspecific pollen transfer.

Waser (1978a) has shown that when the two common perennial plants, *Delphinium nelsoni* Greene (Ranunculaceae) and *Ipomopsis aggregata* (Pursh) V. Grant (Polemoniaceae), grow together in the dry meadows in the Elk Mountains of Colorado, they generally flower sequentially. The respective blue and scarlet flowers are commonly visited by broad-tailed hummingbirds (*Selasphorus platycercus* Swainson), and during the brief period of overlap in flowering of the two plants, the hummingbirds visit *both* species, carry mixed pollen from both species, and cause interspecific pollen transfer. Flowers of both species during this time of overlap in blooming, as well as potted plants subjected by hand to interspecific pollination, suffer significant (25–50%) seed set reduction relative to the nonoverlap period. This is excellent evidence that the two species compete for hummingbird pollination by way of competitive interaction of the interspecific pollen transfer, and Waser concludes that the reproductive loss of the plants in the period of flowering overlap represents a potent selective force that could maintain divergent flowering times of *D. nelsoni* and *I. aggregata*.

The penalty of overlapping blooming in the unrelated perennials studied by Waser was a reduction in fertility, but in some closely related species the penalty can be still greater. For example, 36 species of annual plants, the clarkias (Onagraceae), grow in semiarid areas of California, and frequently bloom at the same time (MacSwain et al., 1973). These bee-pollinated annuals are vegetatively similar, but their flowers have petals of strikingly different shapes and color. Why have they evolved such different visual signals? Detailed studies of the foraging behavior of bees in the ecological context of different clarkia flowers have not yet been done. We can speculate, however, that since the flower fidelity of bees is based on conditioning to specific signals, then if the different species had similar flower signals the bees would be inconstant. Since clarkia hybrids are sterile, such inconstant foragers would predictably cause mass sterilization in their wake. Variety could thus have evolved to minimize straying. The variety, along with habitat differences and flowering time differences, may now be sufficient to have greatly reduced and perhaps even eliminated this lethal effect of competition. The selective pressure for flower divergence may or may not still be available for our inspection in the *natural* population.

CONSTRAINTS AND CONVERGENCE

A recent study of another group of co-occurring, mostly unrelated plants pollinated also by highly promiscuous pollinators shows, in contrast to the above two examples, a high degree of *convergence*. As previously described by Grant

& Grant (1968), hummingbird-pollinated flowers in western North America are characterized by striking convergence in shape and color. Brown & Kodric-Brown (1979) made a detailed analysis of this pollination system in the White Mountains of Arizona. In this area they observed nine plant species, *Ipomopsis aggregata* (Polemoniaceae), *Penstemon barbatus* (Scrophulariaceae), *Castilleja integra* (Scrophulariaceae), *C. austromontana, Lonicera arizona* (Caprifoliaceae), *Aquilegia triternata* (Ranunculaceae), *Silene laciniata* (Caryophyllaceae), *Echinocerus triglochidiatus* (Cactaceae), and *Lobelia cardinalis* (Campanulaceae). All of these plants have long overlapping blooming time. The flowers of all species are red, have long tubular corollas, and frequently bloom in the same local habitat. All of these flowers were visited indiscriminately in the sequence and proportions in which they were encountered, by at least two common hummingbirds, *Selasphorus rufus* and *S. platycerus.* (Six additional species of hummingbirds overlap geographically with the range of most of the flowers.) With one exception (*L. cardinalis*) to be discussed later, all of the plants also supply similar nectar rewards. Since the close relatives of the plants have strikingly different appearance and are insect-pollinated (Grant & Grant, 1968), the similarities of the different genera must represent a true convergence, either by way of demography or by "coevolution."

What have been the selective pressures for convergence and what mechanisms allow it to exist? These temperate hummingbirds are migrants, and Grant (1966) pointed out that it would be advantageous for all of the hummingbird-pollinated plants in the birds' migratory ranges to employ similar signals and rewards to attract whatever hummingbirds are locally available. A bird conditioned to find rewards at a specific kind of flower would be attracted to flowers of similar appearance at another locality. However, hummingbirds are relatively promiscuous flower visitors, so that there are probably other, more primary reasons. Brown & Kodric-Brown (1979) suggest also that these temperate hummingbirds are intra- and interspecifically territorial so that only one resident bird is reliably present within a local area. There does not appear to be a compelling reason to suppose, however, that this bird could not visit differently appearing flowers. I suggest, instead, that since these pollinators are migrants, they must be generally opportunistic feeders capable of visiting many types of flowers. Unlike resident tropical hummingbirds that differ greatly in bill shape and size (Stiles, 1975; Wolf et al., 1976; Feinsinger, 1978; Feinsinger & Colwell, 1978), the eight potential hummingbird pollinators of the nine plant species are unspecialized and not trophically separated from each other. However, a hummingbird's method of foraging is a relatively specialized behavior in its own right. It may have its own unique constraints, giving few evolutionary options to the plant. First, the high energy expenditure necessitates a high reward. The high nectar reward, in turn, necessitates a long tubular corolla to guard the nectar from nonpollinators. The red color also acts as a nectar guard in rendering the flower relatively invisible to insects while providing a vivid contrast against the foliage to the birds (Grant, 1966; Raven, 1972). A vivid visual display may be particularly important to attract these migratory pollinators from a distance.

There are severe constraints on the architecture of a high-reward flower that is pollinated by a hoverer outside the flower. But the positioning of the stamens

and pistils within the flowers are not so severely constrained, and this suggests that flowers might use different parts of the hummingbird head to transport pollen. (If the *same* part of the head were used, there would potentially be a high percentage of interspecific pollen transfer that might result in the aforementioned loss of fertility observed in *D. nelsoni* and *I. aggregata*.) In the convergent hummingbird-pollinated flowers, *P. barbatus* and *C. integra* have dorsally located reproductive structures and they place most of their pollen on the crown and top of the bill, whereas *I. aggregata*, which has ventrally located anthers and stigma, deposited its pollen primarily on the chin. Where *C. confusa* bloomed together with *P. barbatus*, it deposited its pollen at the base of the bill and front of the crown, whereas the *P. barbatus* pollen was carried farther back on the head (Brown & Kodric-Brown, 1979).

Although using different parts of the body as pollen-attachment sites might work with birds, it cannot work with equal impunity in bees (except with firmly attached pollinia as in Orchidaceae and Asclepiadaceae) that groom pollen from most parts of their body with their legs during successive flower visits. Nevertheless, as indicated by Macior (1974), bumblebee-pollinated plants also partition pollen. Bumblebee foragers do not completely remove pollen from the mid-dorsal and mid-ventral lines of the thorax, and numerous bumblebee-pollinated flowers are specialized to deposit pollen in these specific body parts (Thien & Marks, 1972; Macior, 1974). Indeed, as suggested by Macior (1974), the zygomorphic shape of many flowers (which acts to "guard" the nectar) may be an adaptation to confine and guide the pollinator over the reproductive parts, thus resulting in less wastage of pollen, providing another possible reason for flower convergence.

Exclusive Specialists and Interspecific Competition

Unlike hummingbirds, bees tend to be highly flower-constant, and they do not forage in one relatively predictable way such as by hovering in front of a flower. They land on or enter flowers and collect nectar and pollen by different techniques as required by flower architecture (Macior, 1974; Heinrich, 1976). For example, to collect pollen from wild carrot, *Daucus carota* (Umbelliferae), bumblebees walk rapidly across the flat inflorescence, pressing their body down to pick up the pollen from the surface of the many tiny florets. In order to collect pollen from wild rose, *Rosa* sp. (Rosaceae), they press groups of anthers between thorax and abdomen, vibrate them, turn and grasp another group of anthers, and continue this procedure around the circular perimeter of the flower. To collect pollen from timothy grass, *Phleum pratense* (Poaceae), the bees simply scramble up an inflorescence, easily knocking off the loosely held pollen that then adheres to the body hairs. During each interfloral flight, the pollen is groomed from the body and transferred to the corbiculae. To collect pollen from blue bindweed, *Solanum dulcamara* (Solanaceae), the bees must grasp the hanging flowers with their mandibles and shake the pollen out of the tubular anthers onto the venter (see review, Heinrich, 1979c).

Nectar collecting by bumblebees also involves specialized behavior that is learned by individuals that remain relatively flower-faithful as long as rewards remain available (Heinrich, 1979a).

In order to collect nectar from "open" flowers, such as those of composites,

requires little skill. But to enter a turtlehead, *Chelone glabra* (Scrophulariaceae), flower a bee has to pry apart the partially closed lips of the corolla and crawl deep into the flower and probe near the base of the pistil and the anthers. To collect nectar from jewelweed, *Impatiens biflora* (Balsaminaceae), the individual bee, depending on whether it is a short- or a long-tongued species, may get the nectar by biting into the nectar spur or by entering the flower from the front entrance. In monkshood, *Aconitum* sp. (Ranunculaceae), the ample nectar is held in specialized cuplike nectaries at the tips of modified petals. The nectaries are hidden under a hood of petallike sepals, and only some of the individual bees that encounter these blossoms manage to find this nectar. Those that do find it are highly rewarded and remain highly flower-constant.

Even though any one species of bumblebee may collectively visit a very large range of different kinds of flowers throughout the season and at any one time within a season at a given site, the individuals are relatively flower-constant. By specializing to manipulate the "difficult" flowers, they gain the full economic benefits that the flowers have to offer. These observations suggest that plants could also compete for flower-constant foragers by being different from each other, or "difficult" to handle (Heinrich, 1979c).

To Stand Out or to Conform in Intraspecific Competition

In the system described above, there should be selective pressure for the flowers of one species to contrast strongly with those of another; each species should be unambiguously identified to the pollinator so that it does not stray. Thus, there is selective pressure for diversity between species and conformity within species. Those individuals that are "different" or that do not conform to the pollinator's search image should suffer a reproductive disadvantage, at least until rewards become limiting and the foragers begin to enlarge their sampling and foraging repertory (Heinrich, 1979a).

Selective pressure for conformity within the population presents a potential dilemma, since natural selection acts on the individual and not the group. A seminal paper by Schaeffer & Schaeffer (1979) explores the potential effect of intraspecific competition among *Agave* as well as *Yucca* plants for pollinators. The century plant, *Agave deserti*, produces an inflorescence up to 4 m tall. The pollinators (bumblebees and carpenter bees of *Agave*, and moths of the genus *Tegeticula* for *Yucca*) show preferences for the largest stalks available, and the Schaeffers suggest that this foraging behavior has resulted in the evolution of increasingly greater allocation of resources by the plants to sexual reproduction.

Numerous studies indicate that, given a choice between a plant or inflorescence with many flowers, or one with few flowers, the pollination unit with more flowers enjoys a greater percentage of pollination per individual flower than the one with fewer flowers (Schaal, 1978; Stevenson, 1979; Augsburger, 1980; Schemske, 1980). If unopposed by a competing selective pressure, one would predict that the floral display would increase to, and possibly beyond, the energetic ability of the plant to support such flowers. The ultimate outcome might be an investment in flowering that is so great that it exhausts the plants' food reserves, and results in the death of the plant following flowering. As suggested by the Schaeffers (1979), this is the strategy that has been adopted by many species

of *Yucca* and *Agave*; they are highly visible, and individually identifiable by the pollinators, and they literally knock themselves out to attract pollinators.

The limit on the ultimate floral display should be set not by the energy need of the pollinator, but rather by his wants and expectations, which could be considerably higher than his needs. Indeed, the floral reward of some species of *Agave* are large enough to satisfy not only the energy demands of single bats, but also groups of bats foraging in tight flocks (Howell, 1979). It could be predicted that the plants under the predominating influence of intraspecific competition could ultimately evolve to adopt pollinators with even higher energy expenditure than the bats, or cater to ever-larger flocks of bats that forage as a unit. Such "leap frogging" to adopt progressively larger and energetically more demanding pollinators could be a general evolutionary result of intraspecific competition for pollinators.

Massive commitment to a large floral display is also found in the monument plant, *Frasera speciosa* (Gentianaceae) in the Rocky Mountains (Inouye & Taylor, 1980). This plant also grows in relatively open habitat. Individual plants (inflorescences) that grow to 3 m high are close enough together, however, so that the pollinators (bumblebees) can "compare" and fly to the closest and/or largest neighbor. As in *Agave*, the plants wait many years before reproducing, and flowering is a massive suicidal commitment of all of their reserves. The plants live 20–62 years before flowering and dying (Inouye & Taylor, 1980).

Unlike the plants described above, there are many species that grow and flower in dense crowds. The pollinators then no longer distinguish flowers on the basis of what individual they belong to. Flowers in crowds will be visited, and pollinated, regardless of whether or not they provide food rewards (Henrich et al., 1977), as long as they are in "good company" (with flowers that *are* rewarding or that have recently been rewarding). Under this situation, it would be selectively advantageous to commit as few resources as possible to nectar production, and to throw the resources into seed production instead. This is, for example, the strategy followed by *Lobelia cardinalis*, a mimic blooming in crowds of other hummingbird-pollinated flowers that are highly rewarding (Brown & Kodric-Brown, 1979). Mimicry that has evolved in the context of intraspecific competition may be relatively conspicuous, but "mimicry" in intraspecific competition could be much more ubiquitous, though far more difficult to detect or demonstrate.

The wider plants grow apart, the more pollinators need to be rewarded to fly long distances between them. It is therefore not surprising that most of the high-energy pollination systems are in the tropics, where because of seed predation (Janzen, 1970) and high species numbers, plants are spaced far apart. Conversely, the closer plants are together, the less rewards are needed to feed the pollinators. Furthermore, if the plants are close enough together in a crowd and the pollinator no longer discriminates between individuals, the presentation of rewards should become no longer necessary by individual plants. As explored elsewhere in more detail (Heinrich, 1980), the plant could then either go extinct for lack of pollinators, become autogamous, or become wind pollinated. Most angiosperm plants that are now wind pollinated had insect-pollinated ancestors (Whitehead, 1969). Charles Darwin (1878), who speculated on the evolution of wind pollination,

suggested that it evolved in temperate regions due to scarcity of pollinators. However, there is little evidence for numerical lack of insects in the temperate regions, but if there *were* a lack of pollinators, then this could as readily be an effect of low nectar availability from the plants, rather than a cause for wind pollination.

It must be noted, however, that no one scheme likely always functions to the exclusion of all others. For example, changes of reward within single flowers with many nectaries, or in inflorescences with many flowers, could affect pollination of these flowers. Bumblebees visit and touch inflorescences of clover only briefly, or not at all, if they contain minute nectar rewards, but they stay to visit nearly a dozen florets (as opposed to only 2 or 3), twirling about the inflorescence if the florets contain their full complement of nectar (Heinrich, 1979b), thus presumably transferring more pollen to the flowers.

Can we make broad generalizations in pollination biology? The diverse examples given should perhaps be taken to have interest in their own right. It is clear that no simple models will suffice to explain all of the complexities in any one instance. Good simple models, however, can be abstracts of realities that may or may not apply, or that apply to varying degrees, with specific examples. The selective pressure for any one trait may be multiple and parallel, or they may be conflicting. The range of possibilities, which are not mutually exclusive to account for specific results, are wide.

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Angiosperm Biogeography and Past Continental Movements

Peter H. Raven and Daniel I. Axelrod

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REPRODUCTIVE STRUCTURES AND EVOLUTION IN *LUDWIGIA* (ONAGRACEAE). III. VASCULATURE, NECTARIES, CONCLUSIONS[1]

RICHARD H. EYDE[2]

ABSTRACT

To complete this survey of floral structure the number of *Ludwigia* species prepared anatomically—cleared, sectioned, or both—was increased to 37. In general, nectaries of diplostemonous ludwigias are trichome-covered depressions in the (often raised) summit of the ovary, whereas nectaries of sects. *Dantia, Microcarpium,* and *Miquelia* are convex and hairless. Nectaries of sect. *Ludwigia,* though hairless, are otherwise closer to those of the diplostemonous ludwigias. Vascular features are not useful for grouping *Ludwigia* species. For example: the degree to which petal midveins extend basally differs markedly from species to species, some midveins ending in the vascular girdle, others passing through the girdle to the flower's base. But species that are alike for this trait are too unlike in others ways to be allied. The level at which the major bundles of a *Ludwigia* flower part is not a trustworthy indicator of evolutionary level: in some species, at least, it has more to do with the shape of the flower than with gradual phyletic union of appendages. In some ludwigias large bundles in the locular radii retard dehiscence and ensure slow dispersal of seeds. Onagraceous styles commonly carry one bundle in each locular radius and no others, but some of the ludwigias have a second set in the septal radii at the style's base, apparently an archaic trait. *Ludwigia* is the only onagraceous genus in which ovules are supplied by central as well as by transseptal bundles, a peculiarity linked functionally with deeply intrusive placentas and maybe with pollen tetrads. To account for this dual supply—at the same time for *Ludwigia*'s oddly placed nectaries and lack of a floral tube—I argue that epigyny evolved twice in the family, once in the line leading to *Ludwigia* and once in the line leading to all other onagrads.

Gynoecial nectaries and a central ovular supply are among the traits that set *Ludwigia* apart from other onagraceous genera. Throughout the family vascular bundles supplying the ovules pass transversely through the septa of the inferior ovary. *Ludwigia* species commonly have additional bundles running up the center of the ovary. The central system is reported here for the first time along with other aspects of floral vasculature deemed to have systematic worth. I shall argue

[1] I thank Peng Ching-I, T. P. Ramamoorthy, and P. H. Raven for criticizing the typescript. The National Science Foundation contributed indirectly, via a series of grants to Raven, by supporting the field work of several collectors. Photographs are by V. Krantz, drawings by A. Tangerini. Typescript prepared by L. Davis and R. Lardner.

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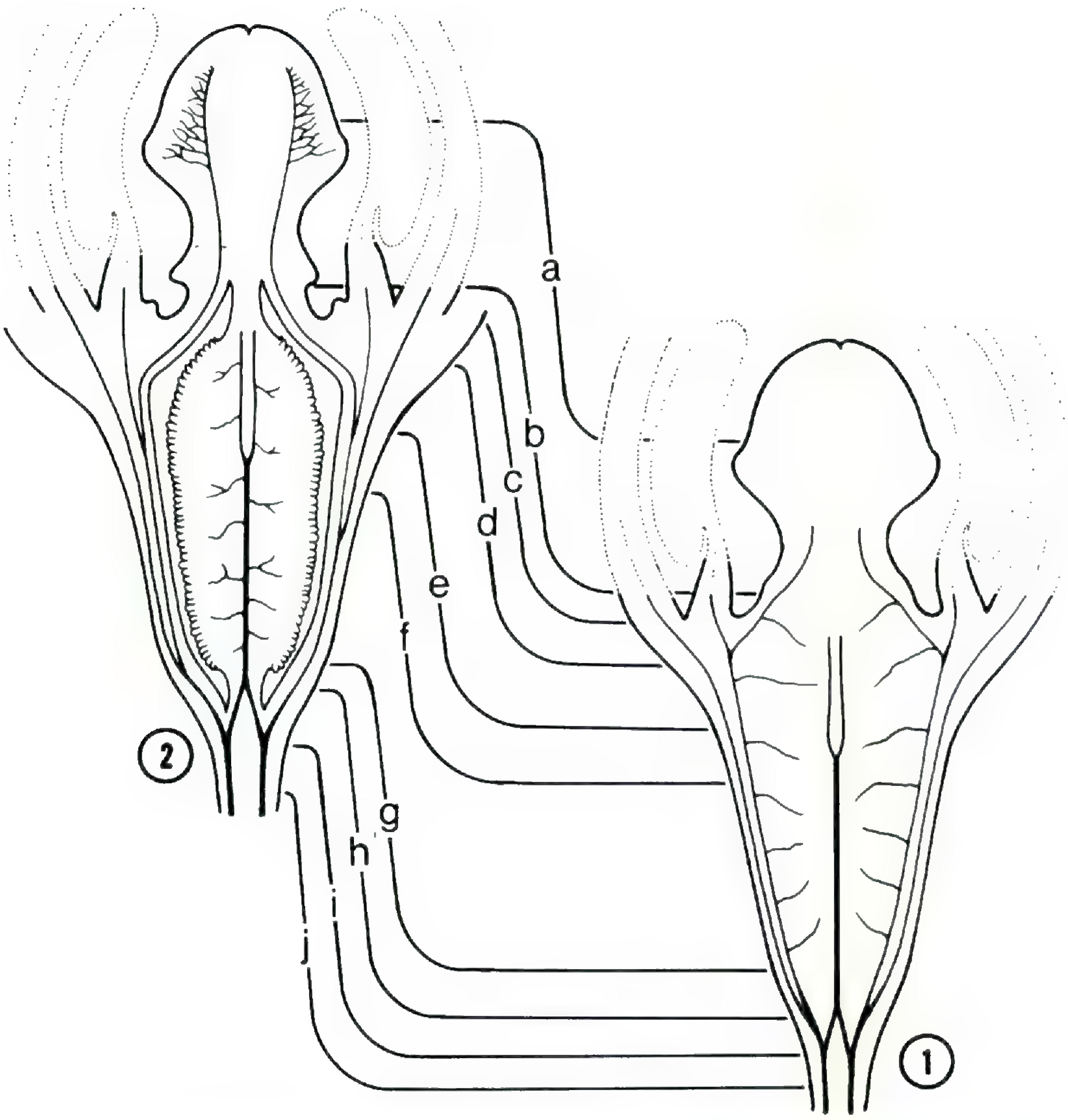
that this system stems from preonagraceous ancestors, offer a concordant explanation for the gynoecial nectaries, and sum up what we can thereby infer about the evolution of the genus.

As far as I know, no one else has looked closely at the floral vascular bundles of *Ludwigia*. Baehni & Bonner (1949: 357) tried to do so but failed for want of good specimens. Saunders's notorious *Floral Morphology* has a short paragraph on *L. palustris* but the observations are superficial. On the other hand, a number of researchers have looked at floral vasculature elsewhere in the family and have described or figured the characteristic transseptal strands (Duchartre, 1842; Van Tieghem, 1868; Barcianu, 1874; Stadler, 1886; Geerts, 1909; Bonner, 1948; Baehni & Bonner, 1948; Kowalewicz, 1956; Eyde & Morgan, 1973; Orchard, 1975). The appearance of onagraceous nectaries is also well known and an occasional observer has noted the odd form and position of *Ludwigia's* nectaries with respect to the others (e.g., Feldhofen, 1933: 564). I do not know that any student of the family has heretofore offered an evolutionary explanation for the oddity unless we count Broekens (1924: 447), who mentioned "Diskusbildung" as one of his reasons for deriving Onagraceae from *Trapa* via *Ludwigia* ("*Jussieua*"). My earlier notion that the gynoecial nectaries of *Ludwigia* are like the interstaminal nectaries of *Lopezia* (Eyde & Morgan, 1973) now seems farfetched, and I have dropped it in favor of the view presented here.

Vouchers for my serially sectioned flowers were tabulated in the first article of this series (Eyde, 1977), where I grouped them into the subgeneric sections then accepted. An updated version of the table would redistribute the species listed under sect. *Myrtocarpus* to accord with Ramamoorthy's (1979) views, and it would include the voucher for another wet collection—*Ludwigia ovalis* Miq., *Boufford 19961* (MO), Japan, sect. *Miquelia*—as well as the additional herbarium specimens cited later in this article. The collections used for sectioning also provided flowers for clearing, some of them cleared whole, some cut beforehand with a razor blade to yield a better view of one part of the vascular system or another. S. Yankowski, who did the technical work for this article and its predecessors, gets good clearings with the following sequence: 5% NaOH, H_2O, Stockwell's bleach (Schmid, 1977), H_2O, chloral hydrate, H_2O, graded ethanol series, xylene. If the flowers have been taken from the herbarium, they are pretreated with Contrad 70 (Schmid & Turner, 1977) and rinsed with H_2O before they are treated with NaOH. Yankowski examines the material often and varies the timing of each step according to the visible progress of the clearing process. The cleared flowers can be kept indefinitely in covered dishes of xylene, though the fluid must be replenished or changed periodically. We use size zero or 00 artists' brushes to manipulate the cleared flowers when examining them microscopically, and we wear the Mine Safety Appliance Company's Comfo II respirator to avoid breathing toxic xylene vapor. To avoid xylene vapor when coverslipping sectioned flowers we mount the coverslips in a portable plexiglass hood with an exhaust attachment (Sanders, 1972: 20–21).

The descriptive comments that follow are based more on sections in some instances, more on clearings in others, depending on the quality of the preparations. Two closely approximated bundles, it should be noted, can seem separate to a greater degree in cleared preparations than in sections. The reason for this



FIGURES 1–2. Diagrammatic sections through 4-merous flower of *Ludwigia peruviana*.—1. Septal plane.—2. Locular midplane. Letters mark levels of cross-sections in Fig. 3. Roughly ×6.

is that the eye follows longitudinal sequences of thick-walled xylem elements when clearings are examined rather than the mixture of xylem, phloem, and associated cells followed in sections. Usually bundles containing few thick-walled elements are more plainly seen in sections than in clearings. I paid no attention to the orientation of the floral vascular bundles, that is, to the relative position of xylem and phloem. Not only is it difficult to identify phloem in some material, but I would expect its position to be uncommonly variable in the Myrtales, where internal phloem is of regular, perhaps universal, occurrence.

Floral vascular systems are often described as if the component bundles must develop acropetally. It is now known, however, that some floral bundles originate in isolation and subsequently extend their proximal ends to previously formed bundles (Lawalrée, 1948; Eyde, 1975; Aziz, 1978). This ontogenetic sequence—isolation first, connection later—can be changed phyletically in ways that would be unlikely or impossible if the bundles extended only acropetally. Accordingly, I have tried to write the descriptive passages without an acropetal bias. My reason for doing so will become clearer when I discuss the petal supply in sects. *Ama-*

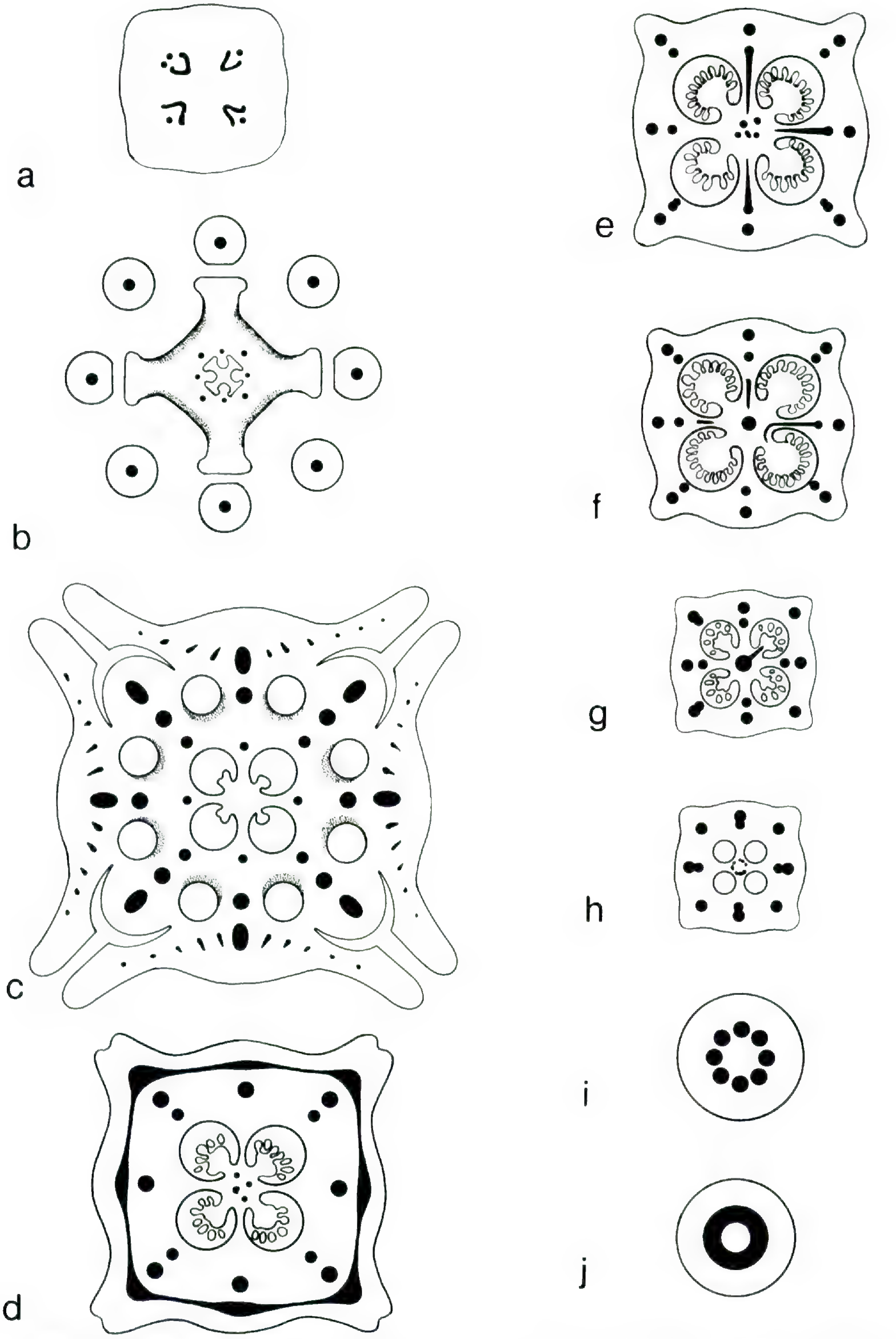


FIGURE 3. Diagrammatic sections through 4-merous flower of *Ludwigia peruviana*. Cf. Figs. 1, 2, and 4. Roughly ×9.

zonia, Oligospermum, and *Seminuda.* The flower of *Ludwigia peruviana* is first because I have a sizeable collection on which to base vascular diagrams (Figs. 1–3) and because it is among the more primitive with respect to floral structure. Flowers of this species can be 4-merous or 5-merous; I chose 4-mery to simplify the diagrams.

Ludwigia peruviana

The most conspicuous bundles in the flower are the sepal midveins. Followed basally they continue through the wall of the inferior ovary in the septal radii, the course of each marked by a broad external rib that can be visible to the unaided eye. Interior to each sepal bundle and in the same radius is a bundle supplying an antesepalous stamen. The paired bundles are close together at all levels (Fig. 1), but they unite only at or below the lowermost level of the locules (see pairs still evident in Fig. 3h).

Petal midveins of this species can also be followed downward into the ovary wall. Each lies in the midplane of a locule accompanied by a bundle supplying an antepetalous stamen. The level at which the stamen bundle joins the basal extension of the petal bundle varies even within the same flower. In my material the junction is always in the lower half of the inferior ovary (Figs. 2, 3g) and in some instances paired structure is evident down to a level below the placentas. This is true only of *L. peruviana*; the junction is at least somewhat higher in all other ludwigias that I have looked at.

At the flower's base, all longitudinal bundles merge in a circle of eight bundles (Fig. 3i)—ten if the flower is 5-merous. Followed deeper into the peduncle the circle becomes a continuous vascular cylinder (Fig. 3j): the level at which this change occurs is probably age-dependent. In some *Ludwigia* peduncles strands consisting only of phloem run through the pith. I have seen such strands in peduncles of *L. decurrens* and *L. pilosa* but not in *L. peruviana.* Similar medullary phloem strands have been found in *Ludwigia* stems (Fukuda, 1967: 352).

All *Ludwigia* species commonly have a pair of bracts below the flower or adnate to the inferior ovary. As monographers have noted, the position of the bracts varies within species and between species, though some species always have higher bracts than others. In *L. peruviana* the bracts (not shown in my figures) usually diverge from the peduncle. Their midveins merge with the peduncle's vascular cylinder in the septal plane, that is, in line with the sepal midvein. In species with higher bracts the median bundles of the bracts may join the sepal supply at or above the base of the flower.

Cross-sections cut slightly below the divergence of sepals and petals pass through a vascular girdle whose segments link the sepal supply transversely with the petal supply. For clarity my diagram (Fig. 3d) shows the whole girdle as if its segments were straight. Actually the segments are somewhat irregular arcs; so a microtome section thin enough to be useful commonly picks up only bits and pieces (but see Fig. 7). To examine the entire girdle one should clear thick freehand sections, as Sporne (1977) did for his article on vascular girdles. Sporne found girdling bundles in 20 families of dicotyledons, including Onagraceae, where I have found few species to be without them. All *Ludwigia* species have a girdle and it is usually conspicuous; indeed, it is the only vascular feature of

Ludwigia that Baehni & Bonner (1949) could discern. The most prominent parts of the onagraceous girdle are the bundle junctions in the locular radii. In *L. peruviana* and some of the other ludwigias one finds in each such radius a vascular plexus where the petal midvein and the girdle join with the most lateral of the sepal bundles (Fig. 8), in other words, with the outermost subsidiary bundles that run through the sepal more or less parallel to its midvein. Some of the other subsidiary bundles of the sepal—and there may be a dozen or more altogether—join the girdle segments at points between the sepal supply and the petal supply, as in *Epilobium angustifolium* L. and a number of other dicotyledons (Sporne, 1977). Minor longitudinal bundles of the petal do not connect directly with the girdle but merge with the midvein in or above the petal's narrow base.

The short style is supplied by four or five major bundles, depending on the flower's merism, these alternating with four or five minor bundles (Fig. 3b). The major bundles can be identified as carpel midveins by their alignment with the locules. Each ends freely high in the stigmatic region after supplying a featherlike network of fine bundles (Figs. 2, 3a, 4). Basally each major style bundle joins the stamen bundle in the same radius, the junction occurring (in *Ludwigia peruviana*) a short distance below the girdle (Figs. 2, 3e). The minor style bundles end distally below the stigma, and their bases join the bundles supplying the antesepalous stamens, the junction occuring just above the girdle.

For simplicity's sake Fig. 1 indicates but a few of the transverse strands that ordinarily pass through the septa of *Ludwigia peruviana*. Ovules number more than 300 per locule in this species, and the transseptal bundles supplying them are plentiful enough that two or three can be seen in most cross-sections. Figures 3e and 3f are idealized in that transseptal bundles seldom if ever run straight through a real cross-section of *L. peruviana*. The upper ones tend to slant downward toward the floral axis, the lower ones upward. Their outer ends join with the antesepalous supply except in the top of the ovary, where a few transseptal bundles connect with the minor style bundles.

In addition to the transseptal supply, the placentas receive bundles from a central system that connects below the locules with the flower's main bundles (Figs. 1–2, 3h). The upper half of this system is a somewhat anastomosing group of bundles having no constant position with respect to locules and septa (Figs. 3d–e). Followed downward these converge in a central column from which fine strands supply the placentas (Figs. 3f–g). Basal connections are with all eight or ten outer bundles, and the strands connecting the central system with the sepal supply seem heavier than those linking it with the petal supply.

On the summit of the ovary of *Ludwigia peruviana* there are four or five nectaries aligned with the petals and the locules. Each is a depression shaped like an inverted and somewhat rounded V (Eyde, 1978: fig. 8) with its arms embracing an antepetalous stamen. Evaporation of nectar is retarded by the many stiff trichomes that emerge all around the margin of the depression and jut out over it to form a sort of thatched roof. Delpino observed as early as 1873 that the trichome cover can bar ants and other small robbers but not a bee's proboscis. Figure 3c shows the nectary as two cavities because the cross-section passes through the arms of the V's (nectariferous tissue stippled); Fig. 3b, passing through the tops of the nectaries, shows each as one concavity. Similar nectaries

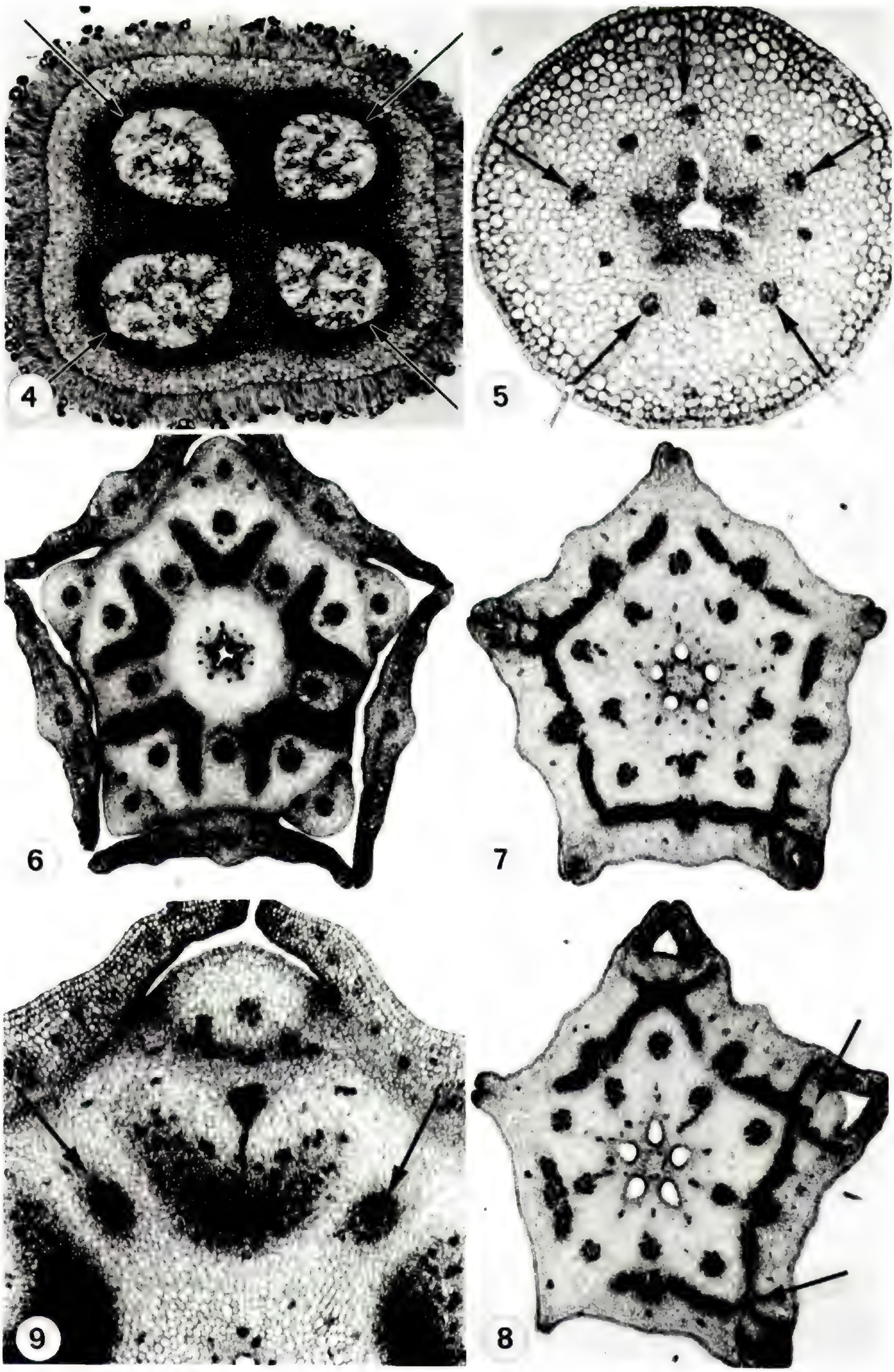
are found in all segregates of the old sect. *Myrtocarpus* (see next paragraph) except *L. densiflora,* in all other diplostemonous ludwigias that I examined, and in some of the haplostemonous ludwigias. The summit of the ovary is less elevated in some of these taxa than in others. Where the summit is not markedly elevated, a cross-section can pass through the whole nectariferous V. Feldhofen (1933) included *Ludwigia peruviana* (as *Jussieua Sprengeri*) in his survey of the structure and secretory function of dicotyledonous nectaries. His fig. 133 is a photographic counterpart of Fig. 3b, and his fig. 134 is a cross-section of one nectary enlarged to show histological details, among them an extensive network of fine bundles connecting basally with all eight stamen bundles.

SIMILAR SPECIES

Emphasizing biosystematic differences, Ramamoorthy (1979) splits the assemblage of species that Raven (1963) assigned to sect. *Myrtocarpus* into seven sections. Except for sect. *Amazonia* (*Ludwigia densiflora*), to be treated later, the flowers of all these sections are outwardly alike, and the outward resemblance is matched by similarity in floral vasculature. I found floral vascular systems throughout the assemblage to be much like that of *L. peruviana* in sect. *Myrtocarpus* sensu stricto.

The vascular differences that do occur do not correlate with the biosystematic differences. To be sure, *Ludwigia foliobracteolata* is like its close relative *L. peruviana* in that the bundles of the petal radii are separate for much of their length (see Fig. 2) and that the style base contains major and minor bundles. But *L. foliobracteolata*'s minor style bundles join the nearest stamen bundles well below the girdle, which is weakly developed when compared with that of *L. peruviana* or with that of almost any other ludwigia. In Ramamoorthy's sect. *Pterocaulon, L. decurrens* has the strongly developed central system seen in ovaries of sect. *Myrtocarpus* s. str., but the central system of *L. erecta,* also in sect. *Pterocaulon,* is nothing but a few slender strands at anthesis. The 8-bundle supply to the 4-merous style base is another detail in which *L. decurrens* resembles *L. peruviana* and *L. foliobracteolata.* Style bundles of the septal radii join the stamen supply below the girdle, as in *L. foliobracteolata.* I found no minor style bundles in my liquid-preserved material of *L. erecta* or in herbarium material of the *Myrtocarpus* species *L. tomentosa*—cleared flowers from *Ratter & Ramos 215* (NY), sectioned flowers from *Dawson 15154* (RSA), and *Gardner 2571* (US), all collected in Brazil. Transseptal bundles of *L. decurrens* and *L. erecta* tend to run straight through the cross-sections, unlike those of *L. peruviana,* perhaps because the *Pterocaulon* species have smaller and more linear ovaries.

The bundles of *Ludwigia latifolia,* now sect. *Tectiflora*'s only species, are much like those of *L. peruviana* except in the locular radii, where they unite at a higher level than they do in *L. peruviana.* In most quadrants a major style bundle joins a petal bundle and an antepetalous stamen bundle in or near the girdle, their downward continuation being one big bundle. Occasionally, the style bundle keeps its individuality for some distance below the girdle, as in the upper left quadrant of fig. 3 of my previous article (Eyde, 1978). In *L. latifolia,* as in *L. peruviana,* there are minor style bundles at the level of Fig. 2b; they seem to join the antesepalous stamen bundles a little below the girdle.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Ludwigia densiflora

Despite its former inclusion in sect. *Myrtocarpus* (Munz, 1942, 1947; Raven, 1963), *Ludwigia densiflora* had long been considered an isolated or aberrant member of that section, and the list of its peculiarities was lengthened recently (Eyde, 1978); consequently, its reclassification as the only species of sect. *Amazonia* Ramamoorthy (1979) is welcome. The distinctness of the species is further indicated by its floral vascular system. Here the petal midveins do not continue downward into the ovary wall, as they do in *L. peruviana* (Fig. 2). Instead, each ends proximally in the girdle. It will be seen that this occurs in some other ludwigias but they are remote from sect. *Myrtocarpus,* old sense or new. *Ludwigia densiflora* is also aberrant in that the outer bundles in the septal radii—that is, the basal extensions of the sepal midveins—develop massive aggregations of fibers. The fibers are laid down in files, apparently through cambial activity starting at the bundle's periphery before anthesis and continuing thereafter. As the fruit matures, the fibers acquire thicker walls and become lignified. In cross-section each aggregation is then a woody arc 15–20 cells deep and more than 50 cells across. The "woody capsule" of *L. densiflora* is consequently oddly constructed, its woody character deriving from the four to six (depending on merism) major vascular bundles. This is another species in which I found no minor style bundles.

There are depressions in front of the antepetalous stamens in *Ludwigia densiflora* as in *L. peruviana*. Here, however, the ovary's summit is flat, not raised—"disc plane" in Munz's treatments—and the depressions are elliptic or crescentic in cross-sections. They are much smaller than the V-shaped nectaries of *L. peruviana* even when allowance is made for the difference in floral size, and in my material they are hairless (Munz, 1974, says subglabrous). I would be led to infer that this highly self-pollinating species (Ramamoorthy, 1979) secretes no nectar were it not for two other observations: the depressions are lined with densely staining cells and they overlie a phloem network.

Sections *Macrocarpon* and *Africana*

As regards floral vasculature, these taxa are much alike even though, all things considered, they are not close allies. They are also much like *Ludwigia peruviana* except that central bundles are not obvious in sectioned flowers of sects. *Macrocarpon* and *Africana*. I judge from examining cleared flowers, however, that central longitudinal strands are not altogether wanting, at least in the lower part

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Figures 4–9. *Ludwigia* flowers in cross-section.—4. *L. peruviana, Steinberg s.n.* Stigma. Section like the one shown diagrammatically in 3a. Same histological zonation is found in all *Ludwigia* stigmas. Four ovate regions contain the feathery vascular supply. Arrows mark locular radii. ×23.—5. *L. peploides, Raven 14529.* Style with major (arrows) and minor bundles. ×100.—6. *L. peploides, Raven 26493.* Ovary's summit not elevated. Section passes through densely stained V-shaped regions underlying the nectaries. ×36.—7. Same flower, 150 μm lower. Shows almost all of vascular girdle in one transverse plane. ×35.—8. Same collection, different flower. Slightly oblique section shows lateral bundles of sepal joining petal midveins (arrows) in girdle. ×35.—9. *L. peploides, Raven 14529.* Transverse bundle connects nectary's vascular network with antepetalous stamen bundle. Antesepalous stamen bundles (arrows) also contribute to nectary supply. ×46.

of the flower. In cross-section a fine, long, central strand is not easily distinguished from short strands connecting the transseptal bundles with the placentas, and dislocated raphides in the central part of the flower may make it impossible to follow any of these bundles for more than three or four microtome sections.

My material of *Ludwigia neograndiflora* and *L. octovalvis*—sect. *Macrocarpon*—has style bundles in the locular radii only. In *L. octovalvis* these bundles link basally with the antepetalous stamen bundles about 1 mm below the girdle in an inferior ovary ("hypanthium") 10 mm or so in length; in *L. neograndiflora* this junction is about a third of the way down the ovary. Similarly, the union of the antepetalous stamen supply with the petal supply is about one-third of the way down the ovary in *L. octovalvis*, about two-thirds of the way in *L. neograndiflora*. As in most ludwigias, bundles supplying antesepalous stamens join the extended sepal midveins near the base of the flower.

I know the two species of sect. *Africana* only as herbarium specimens. My cleared flowers of *Ludwigia stenorraphe* (Brenan) Hara came from *Wood 5341* (US), Natal, sectioned flowers from *Dümmer 2738* (US), Uganda; cleared flowers and sectioned flowers of *L. jussiaeoides* Desr. from *Holst 2972* (US), Tanzania. I found no style bundles in the septal radii of *L. stenorraphe*. The style bundles in the locular radii converge on the antepetalous stamen bundles and the petal bundles a short distance below the girdle. The three bundles come together about a tenth of the way down the inferior ovary. *Ludwigia jussiaeoides* has style bundles in the septal radii, but they are tenuous, each having only two or three tracheary elements in cross-section. I do not know where these slender strands hook up basally because they are hard to follow through the fine network supplying the nectaries; possibly they join basally with that network. As in *L. stenorraphe*, the style bundles of the locular radii join the petal bundles a little below the girdle (less than a tenth of the way down the ovary). Here, however, there are only two bundles involved, for *L. jussiaeoides* is haplostemonous. The antepetalous stamens and their bundles are missing.

Ludwigia perennis

Raven (1963) erected sect. *Caryophylloidea* for the haplostemonous species *Ludwigia perennis* L., citing "ribs on the fruit not being prominent" as one of its distinctions. It is a vascular distinction. Fruits of *L. perennis* have fewer ribs than those of *L. jussiaeoides*, for example, because the ovaries of *L. perennis* are only scantily vascularized in the locular radii. My sections of herbarium flowers—*Morse 275*, Guangxi (US)—show slender strands only two or three tracheary elements thick in some locular radii, no strands in other locular radii. The base of the style has a bundle in each locular radius (none in the septal radii), but I can not tell from my micropreparations how this bundle connects with other parts of the vascular system. The girdle is weakly developed. The central system, much of it concentrated in one large strand, is apparently the important supply to the placentas; transseptal bundles are equally hard to find in microtomed flowers and in cleared flowers. Raynal's (1966) description of *L. perennis* says the summit of the ovary has four glabrous, nectariferous dimples (fossettes) in front of the petals, but her illustration (pl. 18, fig. 4) does not show the dimples nor does it show that the summit is elevated. In my preparations, which include good

longitudinal sections, the summit of the ovary is both glabrous and raised, and the antepetalous quadrants bulge out between the stamens. The dimples, each a shallow depression on the surface of an interstaminal bulge, are evident in some of my preparations but not others.

Endocarp Taxa

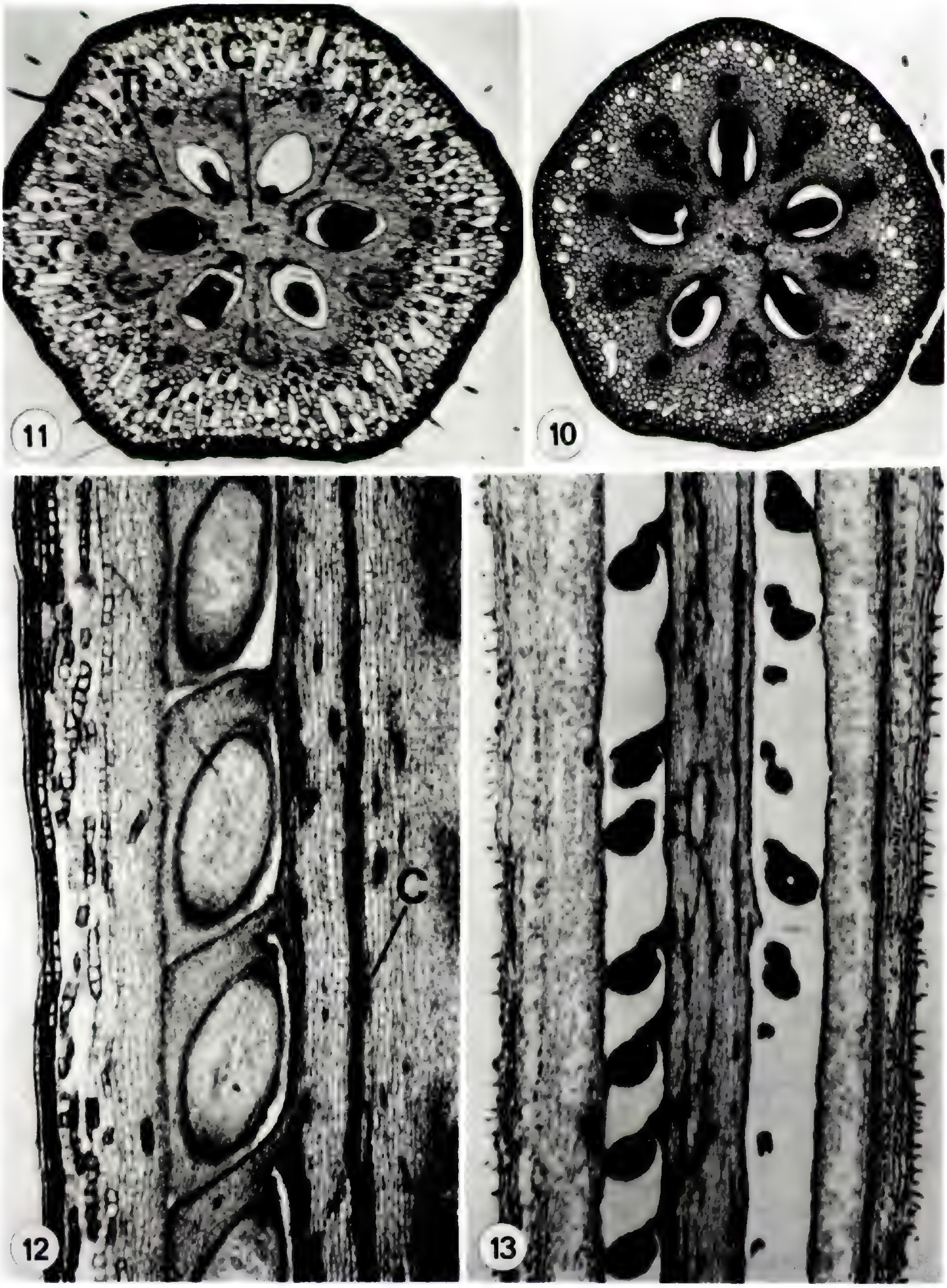
Ludwigias with endocarp-clad seeds fall into two main groups (Raven, 1963; Eyde, 1978). In one of these groups, a natural assemblage comprising sect. *Oligospermum* and *Ludwigia torulosa,* cells linking the locules fuse with outer cells of the testa as the fruit develops. The other endocarp group, with seeds free at maturity, may embrace more than one evolutionary lineage; it comprises sect. *Seminuda* plus *L. abyssinica, L. epilobioides,* and *L. hyssopifolia.*

Floral vasculature of sect. *Oligospermum* differs from that of the ludwigias so far treated in that the two big bundles in each septal radius unite more or less at the median level of the inferior ovary, not at its base. In my material these two bundles commonly merge more or less at the median level of the ovary. In a sectioned flower of *Ludwigia peploides* with columns of 22 ovules or so in each locule the big septal bundles merge opposite the ninth ovule down. In a flower of *L. uruguayensis* with 12–14 1-seriate ovules per locule, they merge opposite the sixth ovule down. Microtome sections taken below this junction show one large bundle in each septal radius, a bundle outlined first by phloem patches, later by a more or less continuous layer of tanniniferous cells. But within each sectioned bundle there is an inner and an outer patch of thick-walled longitudinal fibers; the appearance in a cleared preparation is consequently that of two closely juxtaposed bundles extending to the base of the flower. As the fruit develops, the number of fibers increases, partly by division of bundle parenchyma cells, and the appearance of duality is gradually lost (see the massive bundles in Eyde, 1978: fig. 17).

Petal midveins of sect. *Oligospermum* end basally in the girdle like those of *Ludwigia densiflora.* My preparations of *L. peploides* and *L. uruguayensis* show some of the petal laterals merging basally with the girdle near its junction with the petal midvein. I have not observed this in other ludwigias. Ordinarily, petal laterals merge with the petal midvein at the girdle or a little above it as in *L. peruviana.*

The major style bundles of *Ludwigia peploides* join the antepetalous stamen bundles at the level of the sixth or seventh ovule down. In *L. uruguayensis* the junction is at the level of the third or fourth ovule. Again, these observations are from sections. In cleared material the junctions seem to be lower in the flower. *Ludwigia peploides* has minor style bundles in the septal radii (Fig. 5). Conspicuous in all my preparations from this species, they usually join the antesepalous stamen bundles below the girdle, at the level of the first ovule or a little above it; however, Fig. 8 shows one merging with a stamen bundle a little above the girdle. Oddly, I have not found septal bundles in the styles of *L. uruguayensis* to match those of *L. peploides.*

Ovules of *Oligospermum* species are supplied via the central route (Figs. 10, 12) and by a much-branched network of fine transseptal bundles. A difference with *Ludwigia peruviana* is that all the main transseptal bundles, even the up-



Figures 10–13. Sectioned *Ludwigia* flowers.—10. *L. peploides, Raven 14529.* Cross-section with central bundle supplying ovules. ×46.—11. *L. uruguayensis, Raven s.n.* Cross-section showing central bundle (C) and two transseptal bundles (T). ×33.—12. *L. peploides, Raven 14529.* Longitudinal section of ovary, central bundle prominent. ×50.—13. *L. leptocarpa, Raven 26491.* Longitudinal section of ovary, central supply a network. ×46.

permost ones, rise through the septa at an angle—mostly 30–45 degrees from vertical. As the same is true of most other endocarp taxa, the difference probably relates to the ontogenetic elongation of the inferior ovary in these plants.

Oligospermum ovaries are flat-topped. Accordingly, the V-shaped nectariferous grooves are more or less horizontal with respect to the flower's axis (Figs. 6, 9). Elsewhere in the genus elevation of the summit can vary from one member of a section to another. The character is consistent enough, however, to have a place in Munz's keys, where it aids in parting some closely related species (e.g., *Ludwigia affinis* and *L. leptocarpa*).

In floral cross-sections of *Ludwigia torulosa* the sepal midveins and antesepalous stamen bundles retain their individuality to the base of the flower. The septal pairs do not merge proximally in one large bundle, as they do in sect. *Oligospermum*, at least not in the limited herbarium material that I have examined, and the septal bundles of a mature *L. torulosa* fruit are not massive like those of an *Oligospermum* fruit (compare Fig. 19 with fig. 17 in Eyde, 1978). Petal midveins of *L. torulosa* vary in the way they terminate. Some end proximally in the girdle; others continue down through the ovary wall to the base of the flower. Style bundles occur only in the locular radii. They join the petal bundles in the upper part of the ovary wall or, where a downward continuation of the petal midvein is wanting, continue alone to the flower's base. As in sect. *Oligospermum*, ovules are supplied by the central route and by the transseptal route. The summit of the ovary is divided into five or six swollen lobes by the single whorl of stamens. Traversing each lobe is a deep, gently curved nectary tightly roofed over by a protruding crest of trichomes.

My two collections of *Ludwigia leptocarpa* differ somewhat with respect to vasculature. The big septal bundles retain a distinct duality down to the flower's base in all specimens, whether sectioned or cleared, but there are individual differences in the locular radii. In *Chevalier 21* the major style bundles join the stamen bundles at the girdle or above it. In *Raven 26491* the bundles merge below the girdle—as low as the twelfth ovule down in a column of 75–80 ovules. The petal midveins of both collections end in the girdle and both collections have a well-developed, steeply rising transseptal system. Both collections have bundles in the septal radii of the style base. Those of *Raven 26491* are a series of slender, irregularly oriented strands. Because of their irregularity and spacing, they might well be considered a distal continuation of the transseptal system. In contrast the minor style bundles of *Chevalier 21* are solitary strands like those of *L. peruviana*, but stylar vasculature is not perfectly symmetrical in this collection. The major and minor bundles together are one or two fewer than the combined septal and locular radii, and a bundle can shift from one radius to an adjoining radius when followed through a series of cross-sections. The minor style bundles of both collections merge with stamen bundles at the girdle level or very near it. A nice vascular distinction separates my material of *L. leptocarpa* from that of sect. *Oligospermum*. *Oligospermum*'s central system is largely concentrated in one big strand running most of the length of the ovary, whereas the central system of *L. leptocarpa* is a loose network (compare Figs. 12, 13).

In order to include a second *Seminuda* species, I looked at cleared flowers and sectioned flowers from herbarium specimens of *Ludwigia affinis* (DC.) Hara:

Philipson, Idrobo & Fernández 1620, Colombia (US). As one would expect, floral vasculature is like that of *L. leptocarpa.* The big septal bundles are separate all the way down. Petal midveins end in the girdle. Ovules are supplied by steeply rising transseptal strands in addition to a conspicuous central system that is somewhat more centralized than the reticulate central system of *L. leptocarpa.* Major style bundles, all symmetrically placed, link with the stamen bundles below the girdle, at the level of the uppermost ovule or two. I can not identify minor style bundles in sections of *L. affinis,* and they are just visible enough in my cleared flowers that I can say they are there and nothing more.

Nectaries of *Ludwigia affinis,* like those of *L. leptocarpa,* are hairy inverted V's. Raven (1963) described those of *L. africana* (Brenan) Hara, also in sect. *Seminuda,* as glabrous. A hairless nectary seems out of place in a close relative of *L. leptocarpa* and *L. affinis,* so I looked at rehydrated flowers of *L. africana—Zenker & Staudt 323,* Cameroon (US)—and I found long hairs fringing the nectaries.

Floral vasculature of *Ludwigia abyssinica* A. Rich., sect. *Cryptosperma*'s only species, does not differ greatly from that of *L. affinis* or *L. leptocarpa.* Herbarium flowers from *Baldwin 9734,* Guinea (US), show two bundles in each septal radius all the way to the bottom of the flower. They have neither stamens nor stamen bundles in the locular radii and there are no minor style bundles. Major style bundles merge with the petal midveins in the girdle and stop there; I find no bundles in the locular radii below the girdle, where the wall of the inferior ovary is only about six cells thick. The central system and the steeply rising transseptal system are both well developed. According to Raven (1963) and Raynal (1966), nectaries of *L. abyssinica* are usually fringed with short hairs, but the nectaries of this collection seem to be altogether glabrous.

Septal radii of *Ludwigia hyssopifolia* have the usual two bundles. Despite the narrowness of the ovary, these bundles retain their individuality more or less to the base of the ovary. Central bundles supplying the ovules can be seen dimly in my cleared herbarium flowers, and transseptal bundles can be seen with some difficulty in the microtomed flowers. There are no minor style bundles. The major style bundles join the antepetalous stamen bundles and the extended petal midveins a little below the girdle, where they merge in a single strand that can be followed downward in the locular plane to the flower's base. As the fruit matures, these solitary bundles are more or less enclosed by the hard endocarp tissue that forms around the lower part of each locule, where seeds are 1-seriate. Each bundle then becomes a line of weakness along which the dispersed endocarp units eventually split. This halving of the endocarp unit is unique to *L. hyssopifolia.*

Early in the investigation Raven pointed out to me that fruits of *Ludwigia abyssinica, L. epilobioides,* and *L. hyssopifolia* are not heavily ribbed or fluted like *Seminuda* fruits (see Raven, 1963, figs. 4–6; Ormond et al., 1978, figs. 2–3). The ribbed appearance is an external expression of the eight (or 10 or 12) big bundles directly underlying the surface, those of the locular radii contributing to the effect because they are pressed outward when the hard endocarp units form. This is also the reason for the heart-shaped outline of a *Seminuda* endocarp unit (Eyde, 1978: figs. 35–36): the lobes of the heart take form with the big bundle of the locular radius between them. In *L. hyssopifolia* the bundles of the locular

radii are not seen externally as ribs because in the lower part of the fruit they are at least partially imbedded in the endocarp tissue and in the upper part there is no hard endocarp. Fruits of *L. abyssinica* are not heavily ribbed because they grow from flowers that have no bundles in the locular radii, and the same is true of *L. epilobioides*.

There are no bundles in the locular radii of my herbarium flowers of *Ludwigia epilobioides*—microtome sections from *Lei 993,* Hainan Xingzhengqu, and *Chien 207,* Jiangsu; cleared flowers from the Lei collection and from *Shimadzu Co. s.n.*, Japan (all US). Fruits of this species sometimes have short, irregular bundles in the locular radii, but these are late-developing branches from the outer septal bundles. The ovary wall, like that of *L. abyssinica,* is only about six cells thick in the locular radius (in *L. hyssopifolia,* the thickness is 10–12 cells). Duality of the septal vascular supply is difficult to detect in my cleared preparations; that is, each septal radius seems to contain one heavy strand. Most of my microtomed flowers agree with the cleared flowers, showing the antesepalous stamen bundle and the sepal midvein merging in a heavy strand at the girdle level, but one flower from *Chien 207* has these bundles separate almost to the peduncle. Style bundles, poorly developed and hard to follow, seem to link with the girdle. As this is one of the haplostemonous ludwigias, there are no antepetalous stamen bundles. Petals of *L. epilobioides* are small, and I was not able to find and follow the midveins in microtome sections or in cleared material. With a hand lens, however, I can see petal midveins on some herbarium sheets, and I must assume they end basally in the girdle, because the locular radii are bundle-free below the girdle. The central supply to the ovules is unusually heavy, and it fills much of the ovary's axis; consequently, little or no endocarp tissue develops on the inner side of the locules (Raven, 1963: fig. 6). I judge from the appearance of cross-sections that the endocarp forms completely around the locules in the upper part of the ovary and that the thin inner side then splits as the fruit matures. In the lower part of the ovary, the endocarp seems never to form on the inner side of a locule. Though the transseptal supply is relatively weak in *L. epilobioides,* my cleared flowers show some strands. They are in the lower part of the ovary, and they rise at the sharp angle seen in other species with long, slender ovaries.

The overall similarities of the Southeast Asian species *Ludwigia prostrata* Roxb., alone in sect. *Nematopyxis,* are with the endocarp taxa, even though its fruits do not have a hard endocarp layer. With 1-seriate seeds and no hard endocarp, *L. prostrata* seems to contradict my claim that endocarp formation and single-file seeds are linked developmentally (Eyde, 1978). The wall of the thread-like inferior ovary of this species is so thin, however, that endocarp formation may be out of the question. Moreover, the ovules are not neatly 1-seriate like those of *Seminuda* and *Oligospermum.* My serially sectioned flowers from *Belcher L1-C-498,* Assam (US), show crowding of the ovules in the upper part of the ovary. The condition is reminiscent of *L. epilobioides,* though the two species differ substantially in other respects. Not surprisingly, in view of the thin wall, the inferior ovary of *L. prostrata* has no vascular bundles in the locular radii. The petal midveins end in the girdle, and there are no antepetalous stamen bundles because the flowers are haplostemonous. Furthermore, *L. prostrata* has no style bundles at all in the locular radii. Instead, the style base is vascularized

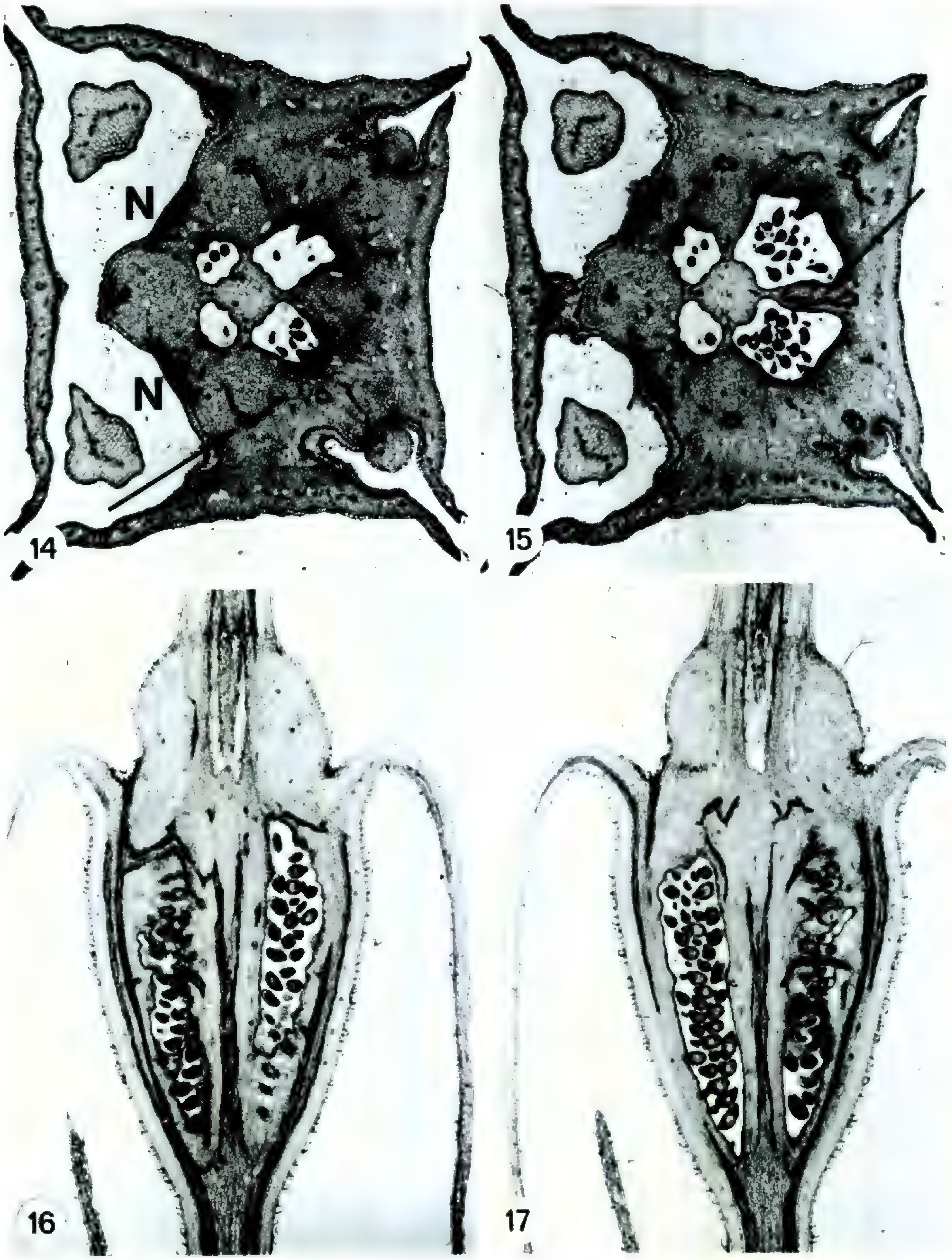
only by bundles corresponding to the minor style bundles of *L. peruviana* or of *L. peploides*. Placentas are supplied by a central system that shows up nicely in my cleared flowers; these, like the sections, are from the Belcher collection. None of my preparations, cleared or cut, show transseptal strands unequivocally. The nectaries are shallow, upright depressions on the ovary's elevated summit. Raven (1963) called them glabrous, but every one I have looked at has a thin skirt of long hairs across the upper edge. One of five microtomed flowers turned out to be 5-merous, a condition not reported before for this ordinarily 4-merous species.

SECTION *LUDWIGIA*

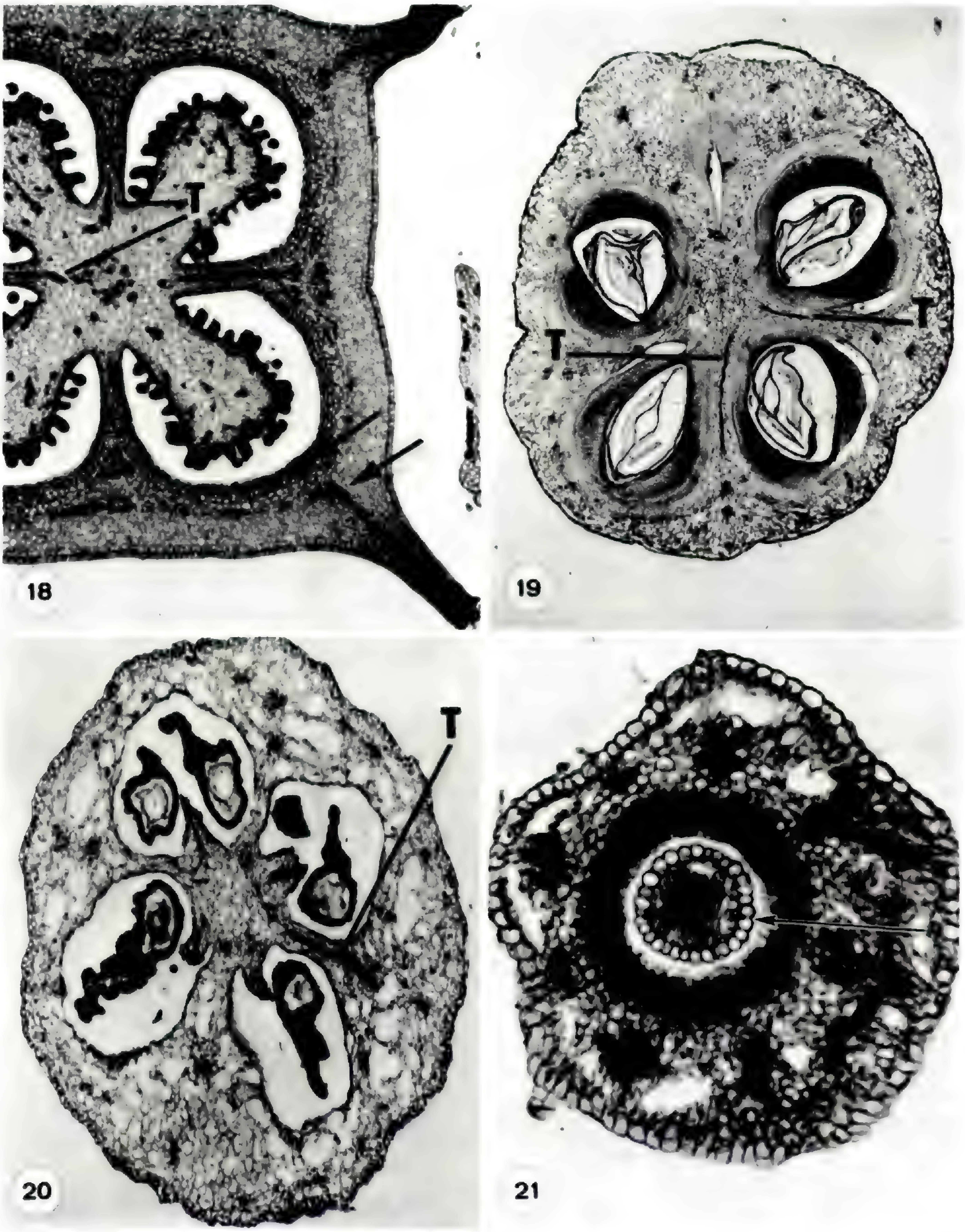
Examining flowers of three of the four species in this haplostemonous section—*Ludwigia alternifolia, L. maritima, L. virgata*—I found almost identical vascular systems. Sepal supply and stamen supply are separate to the flower's base (Fig. 16), as is true of ludwigias in general. In addition the four big style bundles and the four petal bundles can be followed downward as independent bundles for half the length of the ovary or more (Fig. 18). This uncommon condition seems to be related to the angular or winged outline of the inferior ovary. The angles develop below the margins of the broadening sepals, and two bundles differentiating in the same radius are kept apart by the lateral growth that produces the angles. In *L. alternifolia,* where the angles are especially prominent, each is vascularized by a series of short transverse strands connecting like the rungs of a ladder with the petal supply. In the septal radii of *L. alternifolia* short bundles run from the base of the style to each stamen bundle, joining it well above the girdle (Fig. 15), but they are not as well defined or as constant in their occurrence as the minor style bundles of some of the diplostemonous species. The flowers of sect. *Ludwigia* have a strong central system and a transseptal system consisting of a few well-developed transverse bundles (Figs. 16–18). Both systems form early: provascular strands are apparent in a sectioned bud of *L. alternifolia* that was fixed before the ovules had developed. All species of the section have four shallow, but nonetheless prominent, hairless nectaries on the ovary's raised summit. These are abundantly vascularized by a network connected to the four stamen bundles (Fig. 14) and the four major style bundles.

SECTIONS *DANTIA, MICROCARPIUM, MIQUELIA*

Members of these three sections, all herbaceous and haplostemonous, have smaller flowers than most other ludwigias. Some have no petals, but apetaly does not change the position of the stamens; they remain in front of the sepals as if the petals were present. With or without petals, the nectaries are hairless and are rounded rather than depressed. Where they are best developed, they become four prominent hemispheres around a sunken style base (see Mayr, 1969: 235 for floral ontogeny of *Ludwigia arcuata,* a *Dantia* species with protuberant nectaries). Floral vascular systems are similar in the three sections. All species have the downward extensions of sepal midveins and stamen bundles running separately through the ovary to the base of the flower. Styles contain only the four major bundles, and *L. ovalis* (sect. *Miquelia*) may even lack these, for in this species



FIGURES 14–17. Sectioned *Ludwigia* flowers.—14–15. *L. alternifolia, Broome 862.* Oblique sections with sepal diverging.—14. Shows ±transverse bundles linking stamen bundle (arrow) with nectaries (N).—15. Cut 50 μm lower, shows a minor style bundle (arrow) joining a stamen bundle. Both ×19.—16–17. *L. maritima, Arguelles 1,* stamens abscised. Longitudinal sections 30 μm apart showing dual ovular supply; 16, passing through upper part of thin septum on left, shows heavy transseptal bundles linking stamen bundle with placenta and central supply. Note separation of stamen bundle and sepal bundle in ovary wall, also basal linking of central supply with outer bundles; 17, passing through part of septum on right, shows pieces of two large transseptal bundles. Both ×15.



FIGURES 18–21. Flowers of *Ludwigia* and *Gayophytum* in cross-section.—18. *L. alternifolia, Broome 860.* Note transseptal bundles (T), separation of petal bundles and style bundles (arrows), and prominent central supply. ×50.—19. *L. torulosa, Cowan 38886.* Post-fertilization ovary from pressed specimen, one locule abortive. T's mark transseptal strands. Longitudinal bundles of this species are much thinner than those of *L. peploides* and *L. uruguayensis.* ×18.—20. *L. ovalis, Boufford 19961,* with transseptal bundle (T). Ovary wall is aerenchymatous but there is no evolutionary link with aerenchyma of *Oligospermum* ovaries. ×37.—21. *G. racemosum, Raven 26420. Gayophytum* species have no real floral tube but style (arrow) emerges from a depression that has nectariferous tissue on its androecial side. ×114.

the bundles of the locular radii can end distally at the style's base without rising into the style. Nectariferous areas commonly receive a few short branches—mostly supplied by the style bundles—even in the species with less prominent nectaries. The ovules of all species seem to be supplied mainly via the central route, though a transseptal bundle or two can be found in most flowers. The figured cross-section of *L. palustris* in my introductory article (Eyde, 1977: fig. 9) shows a transseptal bundle traversing one of the septa; see also the cross-section of *L. ovalis* in Fig. 20.

The one taxonomically variable feature of floral vasculature worth noting is the degree to which the locular midplane is vascularized. But two species of a section can differ more in this regard than species in different sections, and, contrary to expectation, the flowers with the best-developed bundles in the locular radii—that is to say, in the petal radii—are not those with petals. All my preparations of *Ludwigia alata* (wet collection) have conspicuous bundles running from the style to the girdle, whence they descend to the flower's base. This is also true of most quadrants in the misnamed herb *L. suffruticosa* (US herbarium flowers: *Jones 79,* Florida), though the bundles of the locular radii are much weaker here. Both are apetalous species belonging to sect. *Microcarpium.* In *L. linearis,* a *Microcarpium* species with petals, style bundles merge with petal midveins in the girdle, and the slender strand descending from each merger attenuates and disappears in the ovary wall. *Ludwigia ovalis,* though apetalous, has bundles of the locular radii ending blindly in the ovary wall like those of *L. linearis.* The other apetalous species that I looked at are *L. palustris* (wet collection) in *Dantia* and, in *Microcarpium, L. glandulosa, L. pilosa* (wet collections), *L. lanceolata* (*Harper 1605,* Georgia), *L. polycarpa* (*Bissell & Clarke 245,* Connecticut), and *L. sphaerocarpa* (*Kral 44739,* Alabama). In these species the locular segments of the ovary wall are commonly devoid of long vascular bundles, though they may be lightly vascularized by a few fine, irregular branches from the big septal bundles. Style bundles ordinarily end proximally in the girdle, but in *L. pilosa* I have seen at least one style bundle clearly connecting with a sepal lateral bundle just above the latter's junction with the girdle. In *L. arcuata,* a *Dantia* species with petals, bundles of the locular radii vary markedly even within one flower. Some quadrants have the petal midvein merging with the style bundle in the girdle; in other quadrants the petal midvein joins the girdle but its downward continuation merges with the style bundle below the girdle. Below the junction of *L. arcuata*'s style bundle and petal midvein, there can be a slender strand continuing to the flower's base or a diminishing strand ending blindly in the ovary wall; or, when petal midvein and style bundle merge in the girdle, a downward extension can be lacking.

Vascular Differences Discussed

Except in sect. *Oligospermum,* where the partial loss of duality seems to be ontogenetically and phyletically secondary, the big bundles of the septal radii are separate to the flower's base. This is not true throughout the family. Kowalewicz (1956) found and I have confirmed that the septal bundles of *Epilobium hirsutum* (the D bundles of Bonner, 1948) are not as markedly divided as those of *Oenothera* species, where, Kowalewicz pointed out, the ovary wall is thicker. Simi-

larly, the bundles are double in the large flowers of *Hauya*, single in the small flowers of *Circaea*. But the distinction is not wholly a matter of wall thickness and flower size, for the septal bundles are double even in the threadlike ovaries of *Ludwigia prostrata* and in such small-flowered ludwigias as *L. ovalis*. It depends more, I think, on the timing of development of floral parts relative to each other. Onagraceous petals are slow to develop and in some species they are not even initiated until the antesepalous stamens have begun their development (Payer, 1857: 485; Mayr, 1969). In *L. uruguayensis* ("*Jussiaea grandiflora*") Michaux (1964) found a separate procambium at the site of stamen initiation so early in floral development that only the sepal primordia were present. In other words, the double bundles are there first, before there are two appendages. We can assume that as the flower develops further these strands extend acropetally, retaining their duality, because that is the usual way with procambium.

The vascular diversity of *Ludwigia*'s locular planes contrasts strikingly with the uniformity of the septal planes. In sect. *Ludwigia*, sect. *Macrocarpon*, *L. foliobracteolata*, and *L. peruviana* bundles supplying style, stamens, and petals are discrete in the upper part of the ovary. In *L. hyssopifolia* and *L. latifolia* these bundles unite basally in the girdle and continue downward as one strand. In some other species the petal bundles end in the girdle while stamen or style bundles in the same planes pass by the girdle without merging. There are examples among the haplostemonous ludwigias (*L. abyssinica*, *L. epilobioides*, *L. prostrata*, and to some extent *L. torulosa*), as well as the diplostemonous ludwigias (sect. *Oligospermum*, sect. *Seminuda*, *L. densiflora*). In *L. linearis* and in the apetalous *L. ovalis*, bundles of the locular planes descend to a blind ending in the ovary wall. Most apetalous species have no bundles in the locular radii except the style bundles, these ending basally in the girdle. The diversity is linked in part to the presence or absence of petals and antepetalous stamens in the locular radii, in part to the thickness of the ovary wall. But these correlations do not explain every variant. In *L. arcuata*, for instance, complete bundles are wanting in some quadrants even though petals are present and the ovary wall is not especially thin. It occurred to me at one point that strong or weak development of bundles in the locular planes might be functionally based through a link with nectary size or stigma size, but a scanning of my serial sections turned up no such link. On the contrary, the stigma of *L. pilosa* is bigger than that of *L. alata*, though the latter is the one with complete bundles in the locular midplanes; and *L. alata*, *L. arcuata*, and *L. pilosa* all have well-developed nectaries while differing as to the development of the bundles in the locular midplanes.

Again, I think differences in developmental timing are important for explaining the vascular differences. Presumably, bundles develop along auxin gradients, the sources for the auxin often being a primordium at the distal pole and an already delineated but still differentiating vascular strand at the proximal pole. Ordinarily, the proximal pole is in an acropetally extending longitudinal strand. But in sect. *Oligospermum* and other taxa with the same peculiar petal supply we must assume the angle of the formative girdle is the proximal pole because that is where the midvein ends. The angle can be viewed as a sink getting auxin laterally from the two nearest sepal midveins along lines of intercellular stress. My reading of Michaux's (1964) research on *Ludwigia uruguayensis* suggests an explanation for the vascular difference between the several "peculiar" species and other lud-

wigias, namely, that the peculiar ones produce petal primordia out of the normal centripetal sequence—that is, after stamen primordia have been initiated and vascularized. Mayr's (1969) work showed that the initiation sequence can differ even between closely related species: the sequence is normal in *L. arcuata* but petals follow stamens in *L. repens* Forst. ("*L. natans* Ell."). Possibly the petal midveins of the peculiar species develop basipetally or bidirectionally. This must be true of at least some ludwigias; I do not know how else we would have species with the midveins running through the girdle to terminate blindly below it. In this connection it should be recalled that auxin usually moves basipetally. This is one reason why a pair of closely juxtaposed bundles can run the length of the ovary and not lose their duality; another is that an early action of auxin is to limit the number of cells programmed to divide and then differentiate (Sussex et al., 1972).

In *Ludwigia alata,* where there are bundles in the locular midplanes but no petal primordia to aid in their initiation, the distal auxin sources are probably the marginal meristems of the sepals. In other words, both the wings on the ovaries and the bundles in the wings reflect the strong lateral growth of the sepal primordia. Intensified lateral growth could result from selection pressure involving the persistent sepals as photosynthetic structures—for their ability to pay part of the energy cost of making seeds.

Differences in the way bundles of the locular midplanes interconnect do not help the taxonomist. Of course, the peculiarity in *Ludwigia peploides*—petal midveins ending in the girdle—is found in *L. uruguayensis,* a member of the same section. And the same peculiarity is shared by sect. *Seminuda* and *L. abyssinica,* where fruit structure (Eyde, 1978) indicates common ancestry. But differences between *Oligospermum* fruits and *Seminuda* fruits are so great that the vascular peculiarity must have arisen more than once within the genus. This seems remarkable in view of Sporne's (1976) survey of vascular girdles, for in a score of families with girdling bundles he found only one genus, *Viola,* with petal midveins ending in the girdle or, as he put it, "whose petals derive their entire vascular supply from that of the sepals." Among the onagrads, however, it turns out that the trait is not all that rare. Geerts (1909) and Kowalewicz (1956: 580) found, as I have, that the petal midveins of oenotheras end in the girdle. Fuchsias are variable for the trait. In *F. excorticata* (Forst.) L. f. and *F. paniculata* Lindl. the midveins end in the girdle; in *F. magellanica* Lam. they merge with the antepetalous stamen bundles in the girdle then continue basad as one bundle; and in some fuchsias there is no girdle (my observations). Unlike *Ludwigia, Fuchsia* and *Oenothera* have a floral tube above the ovary, and the explanation that I invoked for the vascular peculiarity—a difference in the timing of the initiation of floral appendages—runs into difficulty. To be sure, there are indications in the literature that onagrads with floral tubes differ developmentally among themselves as ludwigias do. Mayr (1969) found petal primordia and antesepalous stamen primordia arising simultaneously in a fuchsia; whereas Sattler (1973) found normal centripetal initiation of floral parts in another, and Hulbary & Nagaraja Rao (1959) reported the sequence to be sepals, carpels, stamens, petals in an oenothera. The difficulty for the timing explanation is that other oenotheras have normal centripetal initiation (Weisse, 1899; Pankow, 1966; Bunniger & Weberling, 1968; Mayr, 1969), yet as far as I know all have vascular peculiarities.

If there is a functional aspect to the termination of a petal midvein in the

girdle, it escapes me, but other bundles of the locular midplanes have at least one role besides transport. These bundles pass through the ovary wall in such a way as to help or hinder the eventual release of seeds. Geerts (1909: 121) pointed out that the position of the furrow along which each locule of an *Oenothera* capsule will split is established by a median vascular bundle supplying the antepetalous stamen; the bundle disappears, he said, as the fruit wall ripens. Comparable vascular strands in *Ludwigia,* on the other hand, can develop so as to retard dehiscence. The 1-seriate endocarp units of sect. *Oligospermum* are encaged by massive bundles, the one in each locular midplane fitting into a groove on the adaxial side of the endocarp. Much the same can be said of *Seminuda* fruits, though here the vascular structure is weaker. Apparently, fruits of both sections release seeds gradually and irregularly, even when wind-whipped or water-borne. Elsewhere in *Ludwigia* the link between vasculature and dehiscence is complicated by such factors as the shape of the fruit, the thickness of the wall between the bundles, and the strength of the septa. *Macrocarpon* fruits break up lengthwise along the furrows between the eight heavy bundles, and the seeds, being pluriseriate and smaller than those of *Oligospermum* and *Seminuda,* exit easily. Fruits of *L. palustris* can remain intact for months (Salisbury, 1972) even though the mid-locular segments of the fruit wall are paper-thin and devoid of a midvein (Eyde, 1978: fig. 10). In the lower, 1-seriate part of a *L. hyssopifolia* fruit the median bundles do not confine the endocarp units; instead they are deep enough to halve them, presumably providing for faster dispersal. In sect. *Ludwigia* the median bundles strengthen the "seedbox" that keeps the seeds from exiting laterally; evolution of this vascular trait may have provided the selection pressure that led to dehiscence through a terminal pore. Clearly, the genus *Ludwigia* would be a good subject for comparative research on dispersal.

Ludwigia's minor style bundles—style bundles in the septal planes—are a holdover, I think, from the ancestral condition. The presence or absence of these bundles does not simply reflect the size of the style base: style bases of *L. uruguayensis* are at least as big as those of its relative *L. peploides,* yet I found minor bundles well developed in the former, lacking in the latter. And *Hauya* styles, though bigger than those of any *Ludwigia* species, are vascularized only in the locular planes. Indeed, my survey of the family turned up no onagrads, *Ludwigia* aside, in which the style has septal vasculature. In the Melastomataceae the style can be vascularized in either way: some taxa have bundles in the locular planes only and others have them in the septal planes only (Eyde & Teeri, 1967; Subramanyam & Narayana, 1969). Some Myrtaceae have style bundles in both positions (see, for instance, Schmid, 1972a: fig. 30). This condition is probably ancestral because the others are readily derived from it and because it in turn is readily derived from an even older, distally apocarpous condition with three bundles per carpel.

Because of its taxonomic distribution, I judge that the central supply to the placentas is also a retained ancestral trait. I have not seen central bundles anywhere else in the Onagraceae except in *Epilobium nevadense* Munz (in only one of three microtomed flowers) and in one of the more specialized lopezias (Eyde & Morgan, 1973). In both of these instances the central supply must be considered either an anomaly or a phyletically secondary feature. In marked contrast, almost all *Ludwigia* species have a well-developed central system, and taxa with weakly

developed central bundles (*L. erecta,* sect. *Africana,* sect. *Macrocarpon*) are not among the most primitive ones with respect to other features. When I began this investigation I thought the central system must be ontogenetically secondary—made up of late-developing, anastomosing branches from the transseptal bundles. I dropped this notion after I sectioned buds with the floral vascular system at an early stage and found procambium for central bundles already linked to the big outer strands at the flower's base. Now I view the central supply as one mark of *Ludwigia*'s early evolutionary divergence from the ancestral Onagraceae. The myrtalean precursors must have had a central supply to the placentas in common with other syncarpous angiosperms, and the trait has been retained in most modern Myrtales. It disappeared from the main onagraceous line and stayed on with the newly evolving transseptal system only in the line that led to *Ludwigia*. Why did *Ludwigia* alone keep the dual supply? Recall that many of its species, among them the woodier ludwigias of the tropics, have the most deeply intrusive, highly ovuliferous placentas in the family. Natural selection favored the two-way system because reduction to a single set of bundles would have meant smaller placentas, fewer ovules, and a commensurate drop in reproductive success.

Transseptal bundles no longer seem as peculiar as they once did (Eyde, 1967). In recent years species with all or part of the ovular supply crossing the septa have been found in several families, especially in families with inferior ovaries. The list includes Caprifoliaceae (Fukuoka, 1973), Lecythidaceae (Monteiro-Scanavacca, 1974, 1975), Myrtaceae (Schmid, 1972b: 433), Oliniaceae (Rao & Dahlgren, 1969), Rubiaceae (Rao et al., 1964), and Trapaceae (Orchard, 1975). Lecythidaceae, Myrtaceae, Oliniaceae, Onagraceae, and Trapaceae are all myrtalean in one treatment or another (see Briggs & Johnson, 1979: 160), but their transseptal bundles can not be taken as proof of close common ancestry because it is clear that transseptal bundles have evolved repeatedly. Schmid's work with *Eugenia* and *Syzygium,* for example, indicates that the transseptal supply evolved independently in the ancestors of *Eugenia* s. str., though the trait is common elsewhere in subfamily Myrtoideae. And I have learned from conversations with Rubiaceae specialist J. Kirkbride that the rubiads with transseptal bundles are a mixed lot, unrelated by other structural features.

If transseptal vasculature evolved more than once in the Myrtaceae and in the Rubiaceae, it could have evolved more than once in the Onagraceae. I think it did. That is, I infer that *Ludwigia*'s ancestors and the common ancestors of all other Onagraceae developed the trait separately after they diverged. The inference accords with the observation that only *Ludwigia* regularly has both a central system and a transseptal system. It also accords with an idea I shall put forward in subsequent paragraphs, namely, that the inferior ovary evolved independently in *Ludwigia*. It will be seen that an independently evolved inferior ovary accounts for *Ludwigia*'s lack of a floral tube and for the puzzling position of *Ludwigia*'s nectaries.

Ludwigia's Nectaries Explained

Sunken, hair-rimmed nectaries are ancestral in *Ludwigia*. The way in which they are associated with diplostemony and with other ancestral features makes this clear. But these sunken nectaries—indeed all *Ludwigia* nectaries, sunken or

raised—are on the ovary's summit. No other onagrads have nectaries on the gynoecium. Most have them at the base of a floral tube, and the nectariferous tissue is then seen in sectioned material as part of the floral tube because it is on the outer side of the notch where the tube merges with the gynoecium. A few of the onagrads—aside from *Ludwigia*—are tubeless or almost so: *Gayophytum, Gongylocarpus,* species of *Circaea, Epilobium,* and *Lopezia.* Here again, the nectaries are on the appendage side of the appendage-gynoecium junction. In *Gayophytum, Gongylocarpus,* and some circaeas cross-sections through the junction show the base of the slender style encircled by the nectary in such a way that an ancestral tube is easily envisioned (Fig. 21). The epilobiums with free perianth parts above the ovary (sect. *Chamaenerion*) have their stamens united basally in a short stamen tube, and the nectariferous tissue is on the inner side of this tube (Mikhaĭlova, 1964; Kartashova, 1965). Nectaries are also androecial in the tubeless species of *Lopezia.* I once thought *Ludwigia*'s nectaries more akin to *Lopezia*'s than to other onagraceous nectaries (Eyde & Morgan, 1973) but that idea led nowhere, and knowing *Ludwigia* better I have given it up.

How is an evolutionary anatomist to explain the aberrant position of *Ludwigia*'s nectaries? Surely a structure so important for the plant's reproductive success does not move about capriciously in the course of evolution or disappear and reevolve in a different place. The answer, I think, is that nectary position diverged while the ovaries were superior. I envision proto-Onagraceae in which the ovaries stood free within a floral cup, a condition that is retained in the related family Lythraceae. These precursors probably had secretory tissue lining the cup-gynoecium junction, with the tissue more to one side of the junction or the other, depending on the species, for that is just what is found in modern Lythraceae. In *Decodon verticillatus* (L.) Ell., for instance, the nectariferous tissue is unmistakably gynoecial, rising up the ovary to a level above the locule bases (flowers from Anne Arundel County, Maryland, no voucher). *Ammannia coccinea* Rottb., on the other hand, shows a small nectary slightly to the cup side of the junction (Smith & Herr, 1971: fig. 1), and the bat-pollinated flower of *Lafoensia pacari* St. Hil. has a big nectary mostly on the cup side of the junction (Sazima & Sazima, 1975: fig. 3). My sections of *Lythrum salicaria* L. (garden flowers, no voucher) show nectariferous tissue lining the junction and extending up both sides about equally. I have seen densely staining tissue similarly placed in flowers from garden plantings of *Lagerstroemia indica* L.—though as far as I know lagerstroemias no longer secrete nectar—and Mahabale & Deshpande (1957: fig. 30) show a differentiated region extending deep below the cup-gynoecium junction in the lythraceous shrub *Woodfordia.* I think this junction, the notch between gynoecium and surrounding parts, is the ancestral site of nectar secretion for the Myrtales and for many other dicots. From this position, the nectary could extend phyletically up one side or the other; either way would increase the secretory surface. But secondary phyletic migration of the nectary from the outer side and across the junction to the inner side, or vice versa, would likely require more mutations than the initial shift, and would therefore be a less frequent evolutionary event.

The idea that nectaries do not easily pass from one side of the junction to the other is not altogether new. Feldhofen's (1933) survey named several families of dicots in which the floral nectaries are constant in form and position. And Brown's

classic attempt to look at nectaries phyletically postulated two lineages originating in the Theales, one with gynoecial nectaries, the other, including the Caryophyllales and allies, with androecial nectaries (Brown, 1938: 555–556). Although many of Brown's views now seem oversimple, Zandonella's (1972, 1977) thorough investigation of the Caryophyllales sustains Brown's opinion on that group (see also Rohweder & Huber, 1974: 343). Androecial nectaries are indeed a constant feature of the alliance except in the primitive family Phytolaccaceae, where the nectary is between the androecium and the ovary, presumably in the ancestral position. The Caryophyllales are particularly effective for showing constancy of nectary position because flowers of the constituent families have been modified in so many ways. The ovary has become inferior in the Aizoaceae, for example, without shifting the nectary away from the androecial side of the junction. Outside this alliance there are groups in which all members have gynoecial nectaries. In the Gesneriaceae (Wilson, 1974a, 1974b; Skog, 1976) the nectary develops as an annular outgrowth from the very base of a superior gynoecium or as a histologically differentiated region of the ovary wall. The only ambiguity is in the tribe Gesnerieae. Here the nectariferous tissue emerges from the junction where the epigynous part of the flower meets the inferior or partly inferior ovary; it is neither more to the gynoecial side nor more to the androecial side. In the Acanthaceae and the Scrophulariaceae, families close to the Gesneriaceae, nectaries are likewise located at the junction or to the gynoecial side (Feldhofen, 1933: 595; Cosa, 1975). The same is true, I think, of the Crassulaceae and the Ericaceae. In the Rosaceae, on the other hand, the nectary is always part of the floral cup; that is, it is on the androecial side of the junction.

Admittedly, there are a few families in which evolutionary processes probably moved the nectary across the junction. In most Myrtaceae the nectary is on a floral tube or cup (see Kartashova, 1965: 162; Dawson, 1970: 433; Carr et al., 1970)—a sign, perhaps, of common ancestry with the Rosaceae—but sectioned flowers of *Rhodomyrtus tomentosa* (Aiton) Hassk. (from two herbarium collections and from plants cultivated in Florida) show dense tissue that I take to be nectariferous on the summit of the inferior ovary. And R. Schmid tells me the *Syzygium* nectary can be at the junction, on the androecial side of the junction, or on the gynoecial side, depending on the species. I infer that the gynoecial nectary is derived in the Myrtaceae, having migrated phyletically from the floral cup. (As far as I know, there are no gynoecial nectaries among the myrtads with superior ovaries, and these should be closest to the family's ancestry.) Caprifoliaceae is another family with nectaries on both sides of the junction. They are on top of the inferior ovary in *Sambucus* and *Viburnum,* on an epigynous tube in other genera. Some years ago this heterogeneity could have been discounted on the grounds that *Sambucus* and *Viburnum* do not really belong to the Caprifoliaceae, but recent phytochemical work seems to make them bona fide caprifoliads (Bohm & Glennie, 1971; Boulter et al., 1979). If the family is monophyletic, it is likely that the nectary has crossed the junction in one direction or the other. Most Rubiaceae have the nectary on top of an inferior ovary, but a few genera—*Cephalanthus* and *Uncaria* are examples—have the nectary on the androecial side. This does not upset my argument, for I think all such nectaries belong to rubiads with capitate inflorescences, where the flowers have been squeezed, so to speak, into a more slender form. In some of these capitate taxa a little meri-

stematic activity has evolved beneath the nectary, raising it a bit, making it part of the tube, and thereby reducing the flower's girth. The required structural change is slight. More troublesome to me is *Mastixiodendron*, a rubiaceous genus that has no tube, the stamens and petals diverging individually from the gynoecium. I say the genus is troublesome because it is believed that *Mastixiodendron*'s ancestors had a floral tube (Darwin, 1977), because the *Mastixiodendron* ovary, like that of *Ludwigia*, can be partly superior, because I judge from the appearance of microtomed herbarium flowers—*M. pachyclados* (K. Schum.) Melch., *NGF 17392*—that the superior part of the ovary is nectariferous, and because a critic familiar with *Mastixiodendron* could weigh all this and draw a false parallel with *Ludwigia*.

If it can be inferred that *Mastixiodendron* has lost its tube, why should we not think the same of *Ludwigia*? One reason is that *Mastixiodendron* is not as isolated from other Rubiaceae as *Ludwigia* is from other Onagraceae. Indeed, *Mastixiodendron* seems to be a good member of the Chiococceae, a tribe in which other genera show a diminution of the floral tube in varying degree (Darwin, 1977). A more compelling reason for looking at *Ludwigia* differently is the independent evidence—evidence of at least four kinds—that *Ludwigia* is an early evolutionary offshoot. I discussed *Ludwigia*'s 4+-merism in a previous account (Eyde, 1977) and its central vascular system earlier in this article. To these lines of evidence may be added the evidence of flavonoid chemistry and of pollen morphology. J. Averett and P. Raven tell me their initial analyses show an archaic distribution of flavonols and glycoflavones in *Ludwigia* to match the other signs that it is an early offshoot. And *Ludwigia*'s pollen grains have the simple, smooth viscin threads thought to be ancestral for the family (Skvarla et al., 1978). *Ludwigia* species are unspecialized with regard to pollination: they have generalized flowers pollinated by generalized insects (see Estes & Thorp, 1974). If *Ludwigia* diverged from the other onagrads while the ovary was superior, it need never have been pollinated by anything but insect generalists, and it need never have had much of a floral tube—just a modest cup in keeping with its myrtalean ancestry and that disappearing as the ovary became inferior. Indeed, the making of a floral cup would be wasteful if the ciliated depressions on the gynoecium secrete and hold enough nectar to ensure pollination.

The realization that *Ludwigia* need never have had a floral tube beyond the ovary is a turnabout. Before I began to work on this article I thought all present-day onagrads had ancestors with floral tubes. This in turn implied that the ancestors of all present-day onagrads had coevolved with hummingbirds, an implication at odds with the fossil record because onagraceous remains can be found from the Lower Paleocene onward, whereas there were no hummingbirds, it is thought, until the Eocene Epoch or later (Sussman & Raven, 1978). The record seemed to require "an extinct group of insect-pollinated Onagraceae, older than all bird-pollinated Onagraceae" (Eyde & Morgan, 1973: 785–786). Though that requirement is met in principle by my new interpretation, the old insect-pollinated Onagraceae are not all extinct: *Ludwigia* survives.

Diagramming the Dubiosities

Figure 22 is meant to show some of the changes that took place as *Ludwigia* diversified. It combines my thoughts on *Ludwigia*'s evolution with those of Raven

and his coworkers (Raven, 1963, 1980; Skvarla et al., 1978; Ramamoorthy, 1979; Raven & Tai, 1979). Some parts of the diagram are more speculative than others. For example, the placing of *L. hyssopifolia* is somewhat arbitrary, whereas the central position of the *Myrtocarpus* complex is well founded. Relative size of the lobes roughly reflects the number of species surviving in the corresponding taxa, but the distance between points on the diagram is not supposed to suggest relative lapse of time between evolutionary changes. The diagrammatic derivation of one group from another should not be taken too literally. Deriving sect. *Ludwigia* from the *Myrtocarpus* complex does not mean the ancestors are among the extant species. It means I have in mind forebears that would fit fairly well into the *Myrtocarpus* complex if we could recall them from the past.

"*Myrtocarpus* complex" is my term of convenience encompassing sect. *Myrtocarpus* s. str. and two related sections, *Michelia* and *Pterocaulon*. In this complex and nowhere else in *Ludwigia* are found woody perennials with diplostemonous flowers—some of them 4+-merous—and relatively unspecialized fruits. The ovaries often have high summits and longitudinal sections show they can be slightly superior (see pls. 28, 30 in Micheli, 1875). Structurally most primitive within the complex are shrubby, outcrossing perennials of sects. *Michelia* and *Myrtocarpus*. Except for *L. nervosa* (Poir.) Hara, however, these species are polyploids (Ramamoorthy, pers. comm.). *Pterocaulon* species retain the diploid number but stand apart in that they are self-compatible, predominantly inbreeding annual herbs with 4-merous flowers. Ancestral members of the complex must have had the diploidy of this section joined with the 4+-mery and woody habit now largely restricted to sects. *Michelia* and *Myrtocarpus* s. str. Thus the *Myrtocarpus* complex—and the genus as a whole—exemplify a generalization drawn from chromosome numbers in the Winteraceae and other archaic angiosperms: polyploidy can buffer against divergence and paleopolyploids therefore tend to preserve more primitive characters than diploids or low polyploids that have diverged more actively (Ehrendorfer et al., 1968: 349; see also Stebbins, 1980).

Sect. *Oligospermum* diverges first for several reasons. One is that *Oligospermum* fruits lack the spongy layer common among diplostemonous ludwigias, and I think they always did (Eyde, 1978). Diploidy, 5(6)-mery, and well-developed minor style bundles are other signs of antiquity. With *Oligospermum* in this position, the evolution of its 1-seriate ovules and herbaceous habit must be seen as independent events—independent of their evolution elsewhere in the genus—and *Oligospermum*'s solitary pollen grains can be primitively so, predating the tetrads and polyads of sect. *Seminuda* and the *Myrtocarpus* complex. I say *Oligospermum*'s pollen monads *can* be primitive because that would link the *Ludwigia* lineage palynologically with the main onagraceous line, in which monads are undoubtedly primitive. When I look at *Ludwigia*'s flowers functionally, however, I see a nice counterargument. If intrusive placentas and a dual ovular supply are among the earliest specialized features of the *Ludwigia* line, the selective pressure for the divergence of that line must have been increasing the number of ovules per flower. *Ludwigia*'s precursors, the ancestors of all onagrads, had already increased pollination efficiency by evolving viscin threads (Cruden & Jensen, 1979). What would better complete the evolutionary package for the early ludwigias than an early changeover from pollen monads to tetrads

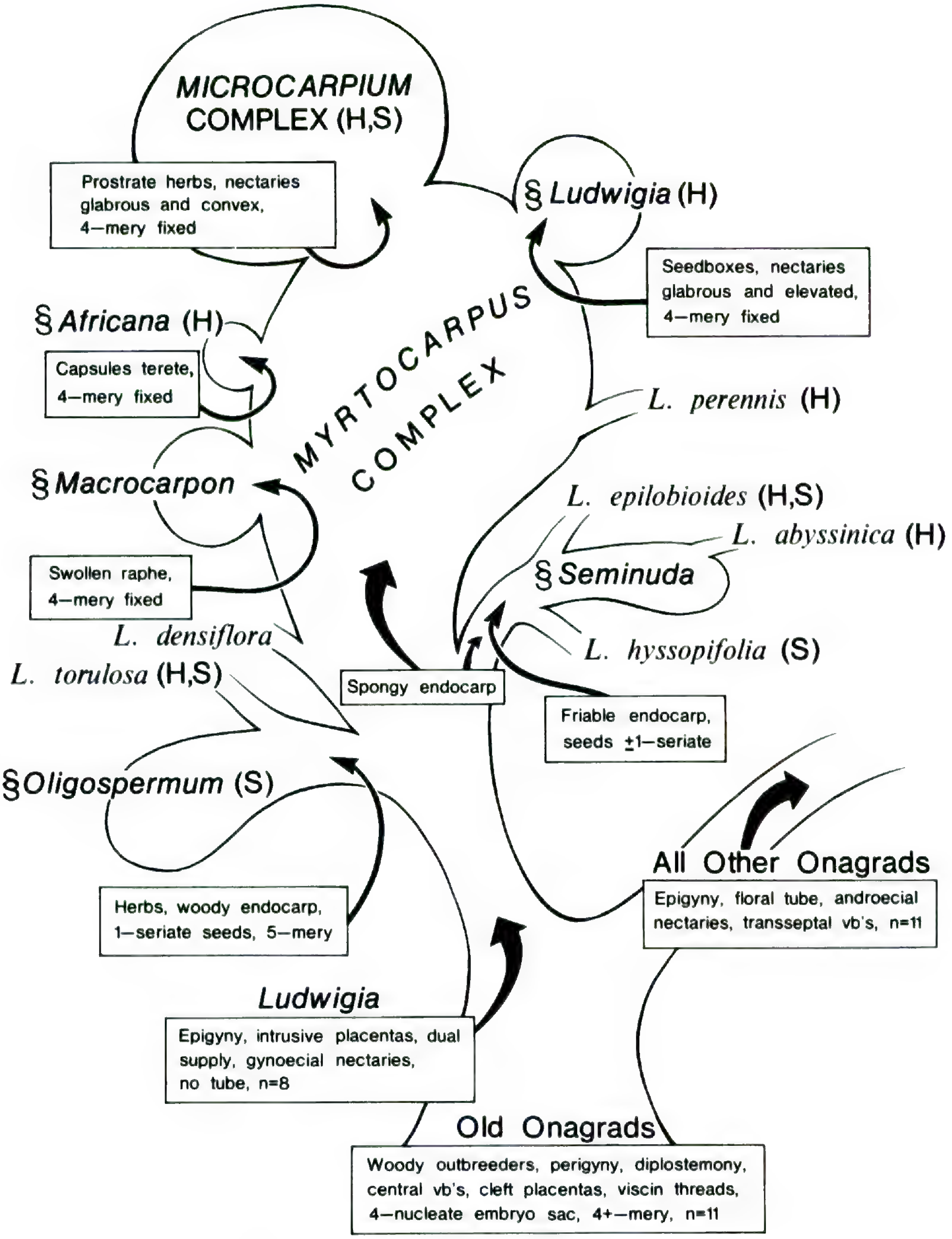


FIGURE 22. Evolution in *Ludwigia*. Some infrageneric sections are left out and some ideas are founded more firmly than others; for details see text of this article and its two forerunners. The gametic chromosome numbers 8 and 11 are ancestral; many Onagraceae now have derived numbers. (S) marks species in which all pollen is shed as monads and groups in which some species (*Microcarpium* complex) or all species (sect. *Oligospermum*) shed only monads. (H) marks taxa that are at least partly haplostemonous. The *Myrtocarpus* complex is treated as wholly diplostemonous, though one species, *L. inclinata*, has some haplostemonous populations.

and polyads? In an outcrossing population, this would provide for the fertilization of more ovules while not requiring that the number of insect visits be increased. Evolution is thought to have taken this course without viscin threads in the Annonaceae and some other families (Walker, 1971: 43). If *Ludwigia*'s early evolution involved a functional linking of pollen tetrads with intrusive placentas and dual ovular supply, we can infer from *Oligospermum*'s retention of the dual supply that monads were abandoned before *Oligospermum* diverged. After *Ludwigia* had diversified further, its subdivisions adopting a variety of dispersal strategies, descendants with reduced placentas could revert to monads without disadvantage and some did.

The ancestors of *Ludwigia torulosa,* a 5-merous, haplostemonous species with *Oligospermum*-like endocarps, would probably fit well in *Oligospermum* as the diagram indicates. Ovaries of sect. *Seminuda* have a spongy zone like the ovaries of present-day members of the *Myrtocarpus* complex. The diagram gives this feature a single origin preceding the divergence of *Seminuda* but following the divergence of *Oligospermum.* All ludwigias up to this level are 4+-merous and diploid. Although surviving *Seminuda* species are polyploid with 1-seriate seeds, ancestral diploids in the lineage may have given rise to *L. hyssopifolia,* a 4-merous species with upper seeds pluriseriate, before 1-seriate seeds became a fixed feature. *Ludwigia epilobioides,* often 4+-merous and with imperfectly 1-seriate seeds, could have a similar origin, but the branching off of this species from the *Seminuda* line would have involved androecial reduction and an increase in chromosome number, *L. epilobioides* being haplostemonous and hexaploid. *Ludwigia hyssopifolia* and *L. epilobioides* could be placed differently in the diagram. One could, for example, attribute primitiveness to their solitary pollen grains (*Seminuda* pollen is in tetrads) and argue that each acquired its fruit and seed characters independently of the other and of the *Seminuda* line. The way I place them is simplest because friable ("corky") endocarp tissue is made to evolve only once, but I am not at all sure that is the way it was (Eyde, 1978: 674). The position of *L. abyssinica* is less doubtful. In all respects it looks like a haplostemonous derivative of sect. *Seminuda.*

In making *Ludwigia densiflora* an offshoot from the ancestral members of the *Myrtocarpus* complex, I have in mind that it retains at least two of *Ludwigia*'s old traits, diploidy and 4+-mery. The *L. densiflora* ovary has no spongy layer. I guessed in an earlier article that the spongy character has been lost, but the ovary could be primitively without a spongy layer if the forerunners of this aberrant species branched off early enough. *Ludwigia latifolia,* not included in the diagram, would be made a more recent offshoot from the *Myrtocarpus* complex. Like *L. densiflora,* it lacks a spongy layer. Here I judge the likelihood greater that the spongy layer has been lost because *L. latifolia* seems much closer than *L. densiflora* to extant *Myrtocarpus* species.

Macrocarpon is made a fairly early-diverging section despite its advanced features—4-mery and the peculiar swollen raphes on its seeds—for it is an outbreeding group with some diploidy in it that stems from old, long-departed diploids, not from modern sect. *Pterocaulon.* Floral vascular bundles are separate to an unexpected degree in *Macrocarpon,* a point of similarity with *Ludwigia peruviana* and *L. foliobracteolata* in *Myrtocarpus* s. str. In addition, there are

fossils to suggest that *Macrocarpon* species are not neophytes. *Ludwigia* seeds with big raphes have been found in the Middle Miocene Fasterholt brown coal of Jutland (Friis, 1980). Though *Macrocarpon* is mostly tropical, it would not be altogether out of place in the Danish Miocene: as a whole the Fasterholt assemblage is like the present flora of our southeastern states (Friis, 1975), at the northern end of the *Macrocarpon* range.

The diagram makes the origins of sect. *Ludwigia* and the *Microcarpium* complex (sects. *Dantia, Microcarpium,* and *Miquelia*) more recent than that of sect. *Macrocarpon*. Actually, one can say for sure only that, as regards such traits as haplostemony and modified nectaries, these groups are more highly evolved than *Macrocarpon*. Hybridization experiments confirm the genetic affinity of the three sections of the *Microcarpium* complex (Peng Ching-I, unpubl.), and a common origin near sect. *Pterocaulon* seems possible. Crosses have also been tried between members of sect. *Ludwigia* and members of the *Microcarpium* complex, and seed set has followed some of these attempts (P. Raven, pers. comm.). But seed set alone can not be taken as proof of close kinship because *Ludwigia* may be a genus in which seeds can result from remote crosses: reportedly, seeds have developed from the crossing of *L. leptocarpa,* in sect. *Seminuda,* with *L. octovalvis,* in sect. *Macrocarpon* (Ormond, 1973; attempts to duplicate this at the Missouri Botanical Garden have failed). Furthermore, structural features seem to make the bond between the *Myrtocarpus* complex and sect. *Ludwigia* tighter than the bond between the *Myrtocarpus* and *Microcarpium* complexes. The dehiscence pore in a fruit of sect. *Ludwigia* is much like the comparable region of *L. peruviana* or one of its allies (Eyde, 1978: figs. 7, 8). And the nectary of sect. *Ludwigia,* though hairless, is like a *Myrtocarpus* nectary in that it is more or less upright and can be at least slightly depressed. If we read these resemblances as signs of kinship, we may then ask whether sect. *Ludwigia* was an offshoot from the line that led to the *Microcarpium* complex and whether sect. *Ludwigia*'s nectary shows a stage in the evolution of the *Microcarpium* nectary. I think not; that is, I judge that the two groups differ enough to have arisen independently from the *Myrtocarpus* complex. But the judgment is based on weaker evidence than one would like. A clearer understanding of the evolution of glabrous nectaries from hairy ones would help. The only thing clear about that now is that it happened more than once.

The nectaries of *Ludwigia perennis,* for example, are like those of sect. *Ludwigia,* but the similarity doubtless results from parallel evolution, for *L. perennis*'s fruits are not at all like sect. *Ludwigia*'s seedboxes. The placing of *L. perennis*—and of sect. *Africana*—relative to other taxa is arbitrary. Both probably originated from the *Myrtocarpus* complex, but floral structure offers no clues beyond that. The position of *L. prostrata,* not diagrammed, is even more uncertain. Emphasizing the absence of major style bundles in the locular radii (of the one collection that I looked at!) would make it the only survivor of a very early-diverging line. Stressing the more or less 1-seriate seeds would make it an offshoot of the *Seminuda* line. Or perhaps it is still another specialized descendant of the old diploids of the *Myrtocarpus* complex.

I picture the ancestral *Ludwigia* flower with little or no floral cup and the ovary only partly inferior, but with placentas already deeply intrusive and many-

ovuled. Still older ancestors, common to all Onagraceae, had superior ovaries; they also had cleft placentas with ovules roughly 2-ranked as in modern *Hauya* and some fuchsias. The styles had bundles in both the septal radii and the locular radii. Sepals, petals, and stamens ended basally in a floral cup and nectaries were at the junction where the cup met the base of the gynoecium. These proto-onagrads lacked the inferior ovary, one of the traits by which the modern Onagraceae are separated from, say, the Lythraceae; however, we can assume they had already acquired onagraceous pollen features, the onagraceous embryo sac, and diplostemony because those traits are found in both the *Ludwigia* line and the main onagraceous line. Flowers became epigynous in each of these daughter lines after they diverged, and in the *Ludwigia* line the nectaries shifted to the gynoecium while the floral cup, its adaptive value diminishing as gynoecial nectaries improved, was lost. An earlier diagram by Broekens (1924: 487) agrees with mine as to the antiquity of *Ludwigia*. But *Ludwigia* ("*Jussieua*") is not, as Broekens thought, the *Stammvater* of the other Onagraceae. It is the *Stammschwester*.

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SYSTEMATICS AND BIOLOGY OF *HOMERIA* (IRIDACEAE)[1]

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ABSTRACT

Homeria is native to southern Africa, where its center of speciation and variation is the western Cape coastal mountain belt and immediate interior, an area of mediterranean climate. Only one species, *H. pallida* occurs exclusively outside the winter rainfall area of the Cape Province, and it ranges widely across the winter dry highland grassveld of southern Africa. *Homeria* belongs to a group of corm-bearing, bifacial-leafed genera of Old World Iridoideae-Irideae and is closely related to the African genus *Moraea*. It comprises mainly large-flowered outcrossing species adapted either to fly or bee pollination, but a few species are self-compatible and autogamous, including three in which complex heterozygosity occurs. In this study, the first revision of the genus since *Flora Capensis* (1896), in which six species were admitted, *Homeria* is divided into four sections. Thirty-one species are recognized of which ten are described here for the first time. Basic chromosome number is $n = 6$ and the genus comprises mostly diploid species, with a few polyploids; three species exhibit aneuploidy, $2n = 10$, 9, and 8. First chromosome counts for a few species are presented, as well as new counts for several others.

Homeria is a moderate-sized genus of Iridaceae native to southern Africa and occurring in the countries of Botswana, Namibia (South West Africa), Lesotho, and South Africa (Fig. 1). It is related to and perhaps derived from the large African genus *Moraea*. Widespread and fairly common throughout its range, *Homeria* is strongly concentrated in the winter rainfall region of the Cape Province. Most species have large brightly colored flowers and are outcrossers with a strong incompatibility system, but a few, smaller-flowered species are autogamous. *Homeria* is important economically as all species are believed to be highly toxic and are a significant cause of stock losses in southern Africa. In spite of its importance, *Homeria* has been little studied in the past and has remained greatly misunderstood, partly owing to the careless way in which specimens have been prepared, and partly to the rather small differences between species. Since Baker's (1896) treatment in *Flora Capensis* in which only 6 species were recognized, over 25 species were added, rather piecemeal, by Rudolf Schlechter (1900) and H. M. L. Bolus in the period 1920–1938. Recent redefinition of *Homeria* (Goldblatt, 1980a) has resulted in the transfer of five species from the genus, three to *Moraea* and two to a new genus, *Rheome*. Several species described by H. M. L. Bolus are reduced to synonomy here, while 10 new species are added, making a total of 31 species of *Homeria* recognized in this treatment (Table 1).

HISTORY

The first species of *Homeria* was described by Carl Peter Thunberg in 1787 in his *Dissertatio de Moraea*. Here *H. collina* was included in Thunberg's very heterogeneous assemblage of species placed in *Moraea*. This was not, however, the first known record of *Homeria*, for as early as 1678 a figure of a plant,

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TABLE 1. The sections and species of *Homeria* arranged in systematic order.

Section **Namaquana**	14. *H. autumnalis* Goldbl.
1. *H. schlechteri* L. Bolus	15. *H. galpinii* L. Bolus
2. *H. ramosissima* Schltr.	16. *H. collina* (Thunb.) Salisb.
3. *H. bolusiae* Goldbl.	17. *H. minor* (Ecklon) Goldbl.
Section **Stipanthera**	18. *H. longistyla* Goldbl.
4. *H. cookii* L. Bolus	19. *H. patens* Goldbl.
5. *H. marlothii* L. Bolus	20. *H. vallisbelli* Goldbl.
6. *H. pallida* Baker	21. *H. flavescens* Goldbl.
7. *H. britteniae* L. Bolus	22. *H. tenuis* Schltr.
Section **Homeria**	Section **Conanthera**
8. *H. cedarmontana* Goldbl.	23. *H. miniata* (Andr.) Sweet
9. *H. ochroleuca* Salisb.	24. *H. pendula* Goldbl.
10. *H. bulbillifera* Lewis	25. *H. spiralis* L. Bolus
a. subsp. *bulbillifera*	26. *H. fenestrata* Goldbl.
b. subsp. *anomala* Goldbl.	27. *H. tricolor* L. Bolus
11. *H. comptonii* L. Bolus	28. *H. bifida* L. Bolus
12. *H. elegans* (Jacq.) Sweet	29. *H. odorata* L. Bolus
13. *H. flaccida* Sweet	30. *H. fuscomontana* Goldbl.
	31. *H. brachygyne* Schltr.

undoubtedly a species of *Homeria*, was published by Breyne in his *Plantarium Exoticarum Centuria Prima* under the polynomial *Sisyrinchium ex phoeniceo suave rubente flore aethiopicum*. This illustration depicts what seems to be a large-flowered species of *Homeria*, much wilted, to which the artist has given what appears to be a superior ovary like that found in *Tulipa*. The figure is the type of Linnaeus's *Tulipa breyniana*. Lewis (1941) believed the figure to represent *Homeria collina*, and she accordingly made the combination *H. breyniana* (L.) Lewis, to replace *H. collina*. Lewis was correct in identifying Linnaeus's *T. breyniana* with *Homeria*, but I believe she was mistaken in trying to place it to species. The illustration is far too crude and could equally be applied to any one of several *Homeria* species. It was for this reason that I recommended rejecting *H. breyniana* and restoring the use of the name *H. collina* (Goldblatt, 1973).

Only two more species of *Homeria* were described by the beginning of the nineteenth century, both assigned to *Moraea*. These were *M. elegans*, described by Jacquin in 1797, and *M. miniata*, by Andrews in 1804. Then in 1808 Ventenat (1808) erected the genus *Homeria*, basing it on *H. collina*, before any more species of *Homeria* were described. Strangely, however, Ventenat failed to make any combinations in the genus (Milne-Redhead, 1937), though *H. collina* is often attributed to him. *Homeria* was not generally accepted by contemporaries, and Ker (1810) continued to recognize species as *Moraea* (*M. collina*, *M. elegans*, *M. miniata*) while describing in addition *M. spicata* (a synonym of *H. elegans*) in his enumeration of this genus. Salisbury, in 1812, was the first botanist to use Ventenat's *Homeria*, and Salisbury validated the combination *H. collina*, as well as naming a fourth species, *H. ochroleuca*, previously treated *H. collina* var. γ. Robert Sweet also gave his stamp of approval to *Homeria* recognizing the genus consistently in all editions of his *Hortus Brittanicus*. Continental botanists, however, continued to follow Thunberg and Ker in assigning species of *Homeria* to *Moraea*.

Despite accelerated botanical exploration in southern Africa in the mid and late nineteenth century, only some eight species were known by 1896 when Baker produced his treatment of Iridaceae in *Flora Capensis*. Baker in fact admitted only six, with *H. ochroleuca* and *H. flaccida* (as *aurantiaca*) treated as varieties of *H. collina*.

An important step towards understanding *Homeria* came with Schlechter's (1900) addition of five new species, all currently recognized, based on his own extensive collections. Among his collections, now distributed widely among world herbaria, were several more undescribed species to some of which he had given provisional names, e.g., *H. concordiae* for *H. schlechteri* L. Bolus, *H. latifolia*, now *H. odorata* L. Bolus, and *H. tulipifera*, now *H. vallisbelli* Goldbl.

H. M. L. Bolus continued to expand knowledge of *Homeria* beginning in 1920. She subsequently paid special attention to the genus and, working mainly from her own collections and from living plants, she described some 20 species in an 18-year period, ending in 1938. Several of Bolus's species are synonyms of earlier species, the types of which were not available to her, but the majority are currently recognized. A minor contribution to the knowledge of *Homeria* was made by N. E. Brown, who in 1929 described four new species in the Transvaal. All of these species are, I believe, merely forms of the widespread *H. pallida* and are reduced to synonomy here.

The total number of species of *Homeria* had, by 1950, increased to 38, a sixfold increase over the number in *Flora Capensis*. The genus has not, however, been revised since the *Flora Capensis* treatment, and consequently it had become very difficult to name species given the lack of keys and the very scattered literature on the genus.

Recent cytological and crossing data, supported by morphological evidence (Goldblatt, 1980a), has made it seem likely that *Homeria* as defined in the past was an unnatural genus and that it comprised three unrelated groups of species. The blue-flowered species previously known as *H. lilacina*, *H. speciosa*, and *H. rogersii* have now been transferred to *Moraea*, the genus to which hybridization studies supported by morphological similarities had indicated they were allied. The new genus *Rhoeme* was created for the only two *Homeria* species with a basic chromosome number of $x = 10$, *H. maximiliani* and *H. umbellata*. These two species have distinctive corm tunics and a basic chromosome number and karyotype that correspond with those of some primitive species of *Moraea*, and their relationships probably lie here rather than with the other remaining species of *Homeria*, which have a basic chromosome number of $x = 6$.

Geography

Although *Homeria* is distributed over a large part of southern Africa, much of this range is accounted for by *H. pallida* (Fig. 1), which extends in the northwest to Windhoek in Namibia and in the east to Pilgrims Rest in the Transvaal. *Homeria pallida* is a species of the winter dry highveld grassland. It flowers in spring, before the summer rains begin, and depends for its moisture either on scant winter rains, or on ground water in poorly drained, often submarshy situations.

All remaining species grow in the winter rainfall area of the Cape Province,

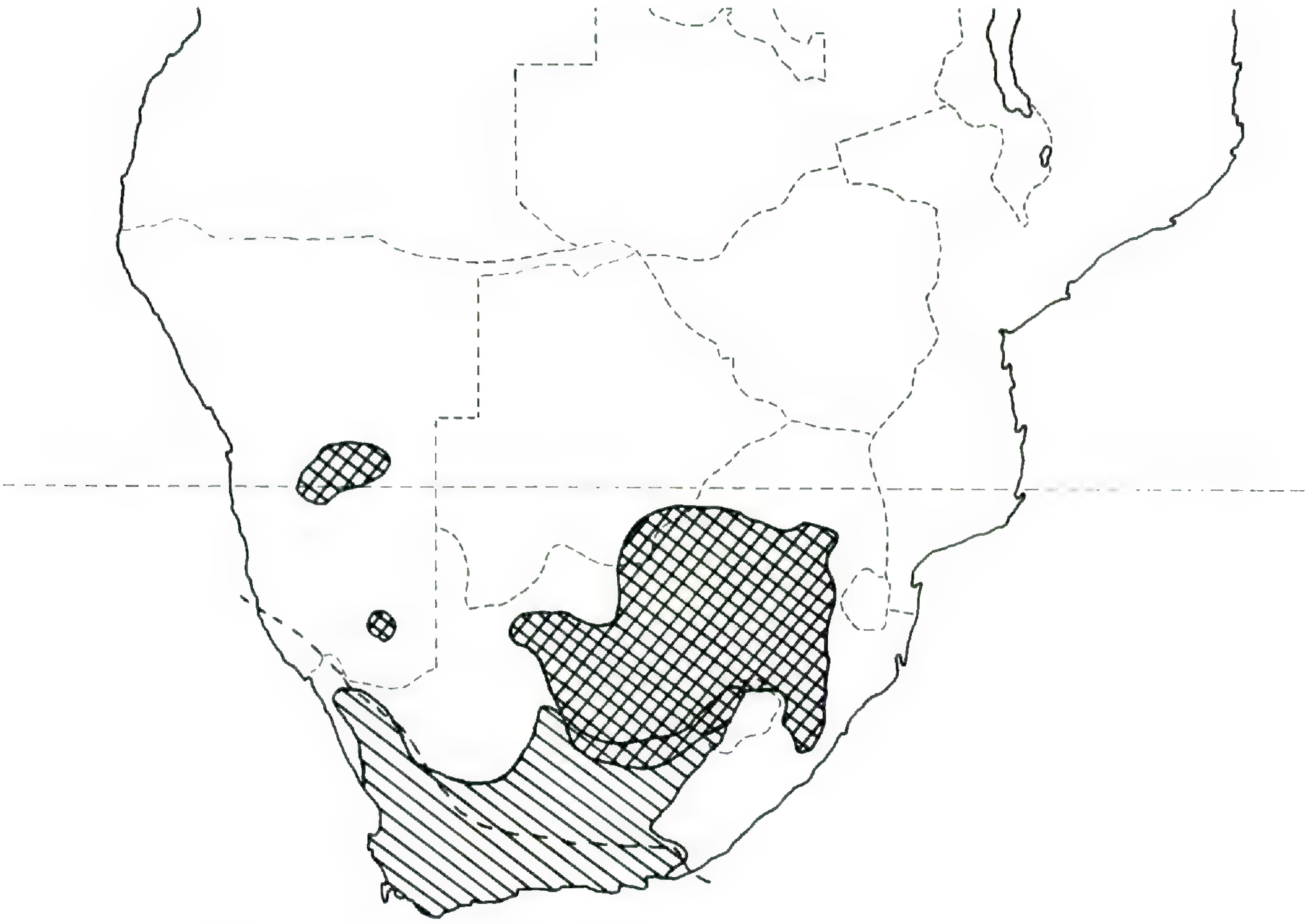

FIGURE 1. Distribution of the genus *Homeria*. The area of effective winter rainfall lies to the south and west of the dotted line. The range of *Homeria pallida* alone is cross hatched.

that is, along the west and southern coasts, or inland in mountainous areas. Only *H. cookii* has any substantial range outside the winter rainfall belt. It is mainly montane and grows in places where there is winter precipitation. *Homeria* has its center of development, both in number of species and in variability, in the mountains of the western Cape (Fig. 2). A total of 12 species occur in the Cold Bokkeveld-Cedarberg-Nardouw Mountain axis. This belt lies mainly in grid 3219 (Fig. 2) with limited extension to the northwest. There are six endemic species here, *H. tenuis, H. flavescens, H. cedarmontana, H. autumnalis H. fuscomontana* and *H. patens*. Altogether 14 species occur in grid 3219, which includes the arid Tanqua basin which lies in the Cedarberg rain shadow, where *H. fenestrata* is endemic. Almost as rich is the grid immediately to the north, 3119 (Calvinia), with ten species. The western edge of this area, the Nieuwoudtville escarpment, accounts for much of the wealth with *H. spiralis* and *H. odorata* endemic locally, and all ten species of the grid occurring here. Species concentration falls rapidly moving east as rainfall decreases towards Calvinia.

Significant concentrations of species occur also in the grids to the south, 3319 (Worcester) and 3419 (Caledon) having nine and eight species respectively. *Homeria comptonii* is endemic to the Caledon area, and its close relative *H. elegans* almost so, with a single record just outside the area.

The western coastal belt is somewhat poorer in species than the more moun-

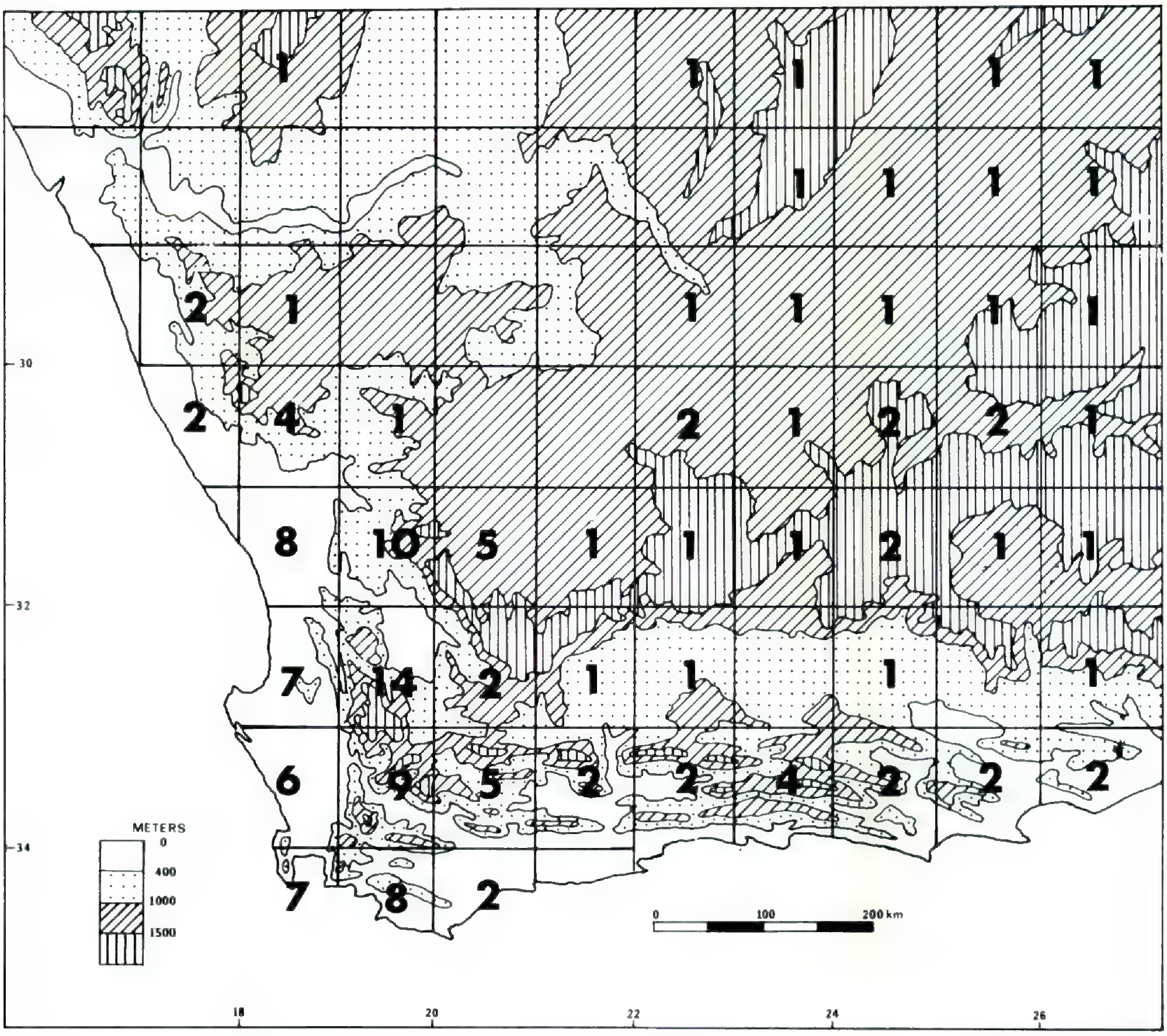

FIGURE 2. Concentration of species of *Homeria* within geographical degree squares. Part of the range of *H. pallida* (Fig. 1) falls outside the map area.

tainous areas immediately to its east, and there are six species in the Cape Peninsula and in the grid to the north. Concentration decreases northward gradually, with eight species in the 3118 grid (VanRhynsdorp), where *H. ramosissima* is endemic, and four in the 3018 grid (Kamiesberg) also with one endemic, *H. pendula*.

The more equable southern Cape coast and mountain belt, with a submediterranean climate, and up to 60% summer precipitation, has in contrast a poor representation of *Homeria*. The species that occur there generally have a wide distribution within the area or occur elsewhere as well. The only locally endemic species occur in the west in the Caledon grid where the climate is most extreme.

The overall pattern of species distribution in *Homeria* indicates that the dissected landscape of the western Cape and its immediate interior with its harsh mediterranean climate and low rainfall has provided the background for much of the speciation in *Homeria*. The geographic component, with its accompanying edaphic and microclimatic variation, is clearly the most significant factor in the evolution of the genus. Only rarely are related species pairs sympatric, and iso-

lating factors such as flowering season (*H. collina-H. minor*) (*H. collina-H. flaccida*) or large differences in flower structure, indicative of pollinator discrimination (*H. miniata-H. pendula, H. bifida-H. odorata*) appear to have assumed an important role in speciation.

Toxicity and Economic Importance

It is generally known to farmers in southern Africa that species of *Homeria* are mildly to severely toxic to stock. The genus is consequently a well known wild plant over most of South Africa, where it is commonly called tulp. In parts of the provinces of Transvaal, Natal, and the Orange Free State members of the related genus *Moraea* are known by the same common name, and several species of this genus are also known to be poisonous, causing similar symptoms in cattle and sheep (Watt & Breyer-Brandwijk, 1962). *Homeria* and *Moraea* together are a significant cause of economic loss due to stock poisoning and in South Africa alone may result in losses estimated at between $2.5–3 million per year from direct deaths, or debilitation (H. Vahrmeijer, pers. comm.). Human deaths have also been recorded, mostly when corms are eaten by mistake for those of edible tulp (*uintjie*), *M. fugax* (syn. *M. edulis*), and perhaps other species.

Several species of tulp (i.e., *Homeria* and *Moraea*) have been tested by veterinarians either in the field or under laboratory conditions at Onderstepoort Veterinary Research Institute and results of several tests have been published, notably by Steyn (1928, 1934). Regretfully, there are either no voucher specimens of the plants studied or the vouchers are now lost or unidentifiable as such so that experimental data on toxicity may not always be correct as to species examined. The systematics of both *Homeria* and *Moraea* have until recently been poorly known, and many species have been known under names now applied to different species. This adds to the confusion about which species are poisonous or whose effects have been experimentally studied.

It is known that the widespread *H. pallida* is extremely poisonous at certain phases of its life cycle. Plants also tested under the names *H. pura* and *H. glauca* may safely be attributed to *H. pallida*. No other species of *Homeria* appears to have been tested as critically for toxicity but Stent & Curson (1922) mention that "*H. collina* and its varieties" and "*H. elegans*" have caused fatalities among stock. It must be assumed that all species are likely to prove toxic, but further critical data are needed to amplify this observation. Other species recorded as poisonous are *H. miniata*, *H. ochroleuca* (as *H. lucasii*), *H. bulbillifera*, *H. flaccida* (as *H. aurantiaca*) (Watt & Breyer-Brandwijk, 1962).

The toxic principle was identified as an alkaloid by M. Rindl in 1924 who named it homeridine. The main toxic action is a heart and nerve depressant. More recently Naudé & Potgieter (1966) reported that the main toxic component is a cardiac glycoside similar to those found in several bulbous Liliaceae that are also poisonous, such as *Scilla* and *Urginea*. Enslin et al. (1966) isolated and described the main toxic principle of *H. pallida*, $1\alpha,2\alpha$-epoxyscillirosidine. It would be of considerable interest to know more about the distribution of this and related alkaloids in *Homeria* and its relatives. The symptoms of tulp poisoning and treatments are discussed by Watt & Breyer-Brandwijk (1962).

Biology

ECOLOGY

Homeria is generally regarded as a weedy genus, a view influenced by the presence of huge numbers of plants of certain species in overgrazed pasture, or in vineyards and plowed fields. In fact, only a few species are normally found as weeds in southern Africa, most important being *H. miniata, H. flaccida,* and *H. pallida. Homeria miniata* is probably native only along the west coast from the Cape Peninsula to Namaqualand, where it is a common, sexually reproducing diploid species. It is now frequent in pastures, vineyards, disturbed roadsides, and abandoned fields well to the east of its native range. The weedy forms are often sexually sterile, sometimes triploid or tetraploid, and they reproduce by means of numerous tiny cormlets produced round the parent corm and at the lower nodes. Wild forms produce only a few quite large cormlets around the main corm.

A second weedy species is *H. flaccida,* which is extremely common, especially in seasonally flooded land on the Cape Flats. It is poisonous and avoided by stock and so, in overgrazed areas near towns, becomes very conspicuous. It is not often found in plowed areas and is apparently easily eradicated, perhaps because it has a poor capacity for vegetative reproduction.

The third important weedy species is *H. pallida,* a plant native in the upper karoo and the highveld grasslands of Natal, the Transvaal, and Orange Free State. In this species there are two distinct cytological races, one with $n = 6$ and one with $n = 4$. The second is derived from the $n = 6$ cytotype, which is basic in *Homeria,* and all of the weedy forms of *H. pallida* I have examined have the derived $n = 4$. *Homeria pallida* has become a weed in part because this very toxic species is avoided by grazing animals. Thus in areas that have been overstocked, *H. pallida* populations grow very large. However, the species is autogamous and the $n = 4$ cytotype is a ring-forming complex heterozygote (Goldblatt, 1980b). These features surely contribute to its success as a weed. While *H. pallida* is common in the Orange Free State, the species is often rare in other parts of its range, and in the Transvaal and Natal is usually restricted to vleis and seeps.

Locally, other species of *Homeria* may also appear to be weeds. This is because, like *H. flaccida* and *H. pallida,* the plants are toxic and avoided by grazing animals. In the absence of competition in grazed areas, they then multiply to an unusual extent. Thus, *H. collina* appears as a weed on the slopes of Devils Peak in Cape Town where buck and deer avoid it. *Homeria schlechteri* is very abundant between Springbok and Okiep in Namaqualand, where much of the natural plant cover has been destroyed.

Homeria has been introduced into Australia, where two species, *H. miniata* and *H. collina* (often misidentified as *H. breyniana* var. *aurantiaca,* i.e., *H. flaccida*), have become established, and are weeds causing serious problems.

In undisturbed habitats the only species normally found in large numbers is *H. miniata,* where populations stretch for mile upon mile in Namaqualand. When other species are found blooming in great numbers, this is a response to some disturbance, fire being the most common stimulant. Species native to the poor,

TABLE 2. Soil preferences of *Homeria* species in the Cape Floristic Region and adjacent areas. The asterisk indicates species not entirely restricted to the soil type indicated.

Species Characteristic of Sandy Soils	Species Characteristic of Clay Soils
H. autumnalis	*H. bifida*
H. bolusiae	*H. bulbillifera* subsp. *anomala**
H. brachygyne	*H. comptonii*
H. britteniae	*H. elegans*
H. bulbillifera subsp. *bulbillifera*	*H. fenestra*
H. cedarmontana	*H. longistyla* * (also very rocky alluvial sites, occasionally sand)
*H. collina**	*H. marlothii*
H. cookii (within the Cape Region)	*H. miniata* (within the Cape Region, also sand in Namaqualand)
H. flaccida	*H. odorata*
H. flavescens	*H. ramosissima*
H. fuscomontana	*H. spiralis*
H. galpinii	*H. tricolor*
H. minor	
H. ochroleuca	
H. patens	
H. tenuis	
H. vallisbelli	

sandstone-derived soils in the southwestern Cape often only bloom after fires. In this category are *H. galpinii, H. cedarmontana, H. autumnalis, H. ochroleuca,* and *H. cookii*. Several other species behave in the same way, e.g., *H. tenuis, H. collina, H. minor,* but they also flower where vegetation cover is sparse without apparent disturbance. Clearing of the vegetation by means other than fire has a similar effect in many species.

Soil type has an important influence on the distribution of *Homeria*. As has been noted for many genera in the Cape Floristic Region, species tend to be restricted either to the characteristic coarse sandy soils, mostly of montane habitats, or to the heavy, more fertile clay soils of the valleys and plains (Dahlgren, 1968; Rourke, 1972; Goldblatt, 1978). This is marked in *Homeria,* where most species are restricted to one soil type. As already mentioned, the strongly fire-responsive species are restricted to sandstone soils. In the Cape Floristic Region and adjacent areas, 16 species are limited to sandy soils (Table 2) while 11 are characteristic of or restricted to heavy clay soils.

REPRODUCTION

Most species of *Homeria* are strongly outcrossing, with self-incompatibility the rule as in other genera of subtribe Homeriinae. Self-compatibility has been observed in the following: *H. collina, H. marlothii, H. britteniae* and *H. flavescens* (one population examined of each), in all four populations of *H. tenuis* and *H. minor* studied, and in plants of several populations of *H. pallida* ($n = 4$ form). In all of these species pollen is shed directly onto the stigmas, thus effecting self-fertilization. Other species in which pollen and stigmas are in direct contact are nevertheless strongly self-incompatible. Pollination in the genus is accomplished by insects and is usually very effective, with most plants of a species producing abundant seed.

TABLE 3. Naturally occurring hybrids recorded in *Homeria*. All examples are intrasectional.

H. flaccida × *H. collina*—sterile, $5n$ (Goldblatt, 1973)
H. ochroleuca × *H. collina*—sterile, $3n$
H. collina × *H. longistyla*—sterile, $3n$
H. comptonii × *H. longistyla*—no data
H. bifida × *H. odorata*—sterile, $2n$

Interspecific hybridization occurs with unusual frequency, and it is usual, rather than exceptional, to find some hybrid individuals wherever species of *Homeria* occur together. These hybrids (Table 3) are sterile, often owing to differences in ploidy levels in parent species. Natural hybrids between *H. bifida* and *H. odorata,* both $n = 6$, grown in the greenhouse, and artificial hybrids between *H. elegans* and *H. miniata,* also both $n = 6$ (Goldblatt, 1973), are also sterile, but the reasons here are not known.

POLLINATION

There appears to be a close relationship between general flower form and pollinating agent. My field observations have indicated the following trends. Species which tend to have the tepals deeply cupped and thus at least partly or entirely include the stamens and style branches usually have a strong, rich, rather overripe scent and are pollinated by flies; sometimes a single fly species appears to be the only visitor. These species secrete nectar at the base of the outer tepal or, in the case of *H. ochroleuca,* rather randomly in the mid-claw region of both the inner and outer tepals. In both cases, the nectar is readily available for lapping/licking. Species on which I have observed fly pollination are *H. collina, H. comptonii, H. ochroleuca,* and *H. odorata.*

In contrast, species with tepals either spreading from the base or in which the tepal claws are held close to the filament column, with the tepal limbs held horizontally, and the anthers and style branches carried well above the tepals are scentless and usually visited by Hymenoptera, mainly bees but also wasps. These species secrete nectar which is concealed in the cavity formed by the tepal claw and filament column. Bees, which I have seen working in large numbers on species with this type of flower, generally alight on the top of the stamen column and rapidly gather pollen. Only occasionally do individual bees probe the base of the filament column searching for nectar. This pattern was noted for three similar and closely-related species, *H. miniata, H. bifida,* and *H. spiralis.*

CONSERVATION

Species of *Homeria* are generally quite common within their ranges and form populations comprising large numbers of individuals. Many grow in places unsuitable for agriculture or land development and thus their future seems secure over much of their ranges. As already mentioned, several species have weedy tendencies and reproduce rapidly, which adds to their security. The few very local species such as *H. cedarmontana, H. autumnalis, H. fenestrata* and *H. pendula* grow in areas remote from human activity and on land unsuitable for

TABLE 4. Chromosome numbers in *Homeria*. Collection and voucher data or previous reference are given in Goldblatt (1980b), but data for a few original counts given here are listed in Table 5. Species marked with an asterisk were previously uncounted.

Species	2*n*	Species	2*n*
**H. autumnalis* Goldbl.	12	*H. longistyla* Goldbl.	12
H. bifida L. Bolus	12, 12 + 4B	*H. marlothii* L. Bolus	24
H. brachygyne Schltr.	12	*H. miniata* (Andr.) Sweet	12 (18), (24)
H. britteniae L. Bolus	12, 24	*H. minor* (Ecklon) Goldbl.	12
**H. bolusiae* Goldbl.	12	*H. ochroleuca* Salisb.	12, 24, 24 + 2–3B
H. bulbillifera Lewis	12, 12 + 1B, 18, 24	*H. odorata* L. Bolus	12
H. cedarmontana Goldbl.	12	*H. pallida* Baker	12, 8
H. collina (Thunb.) Salisb.	24	**H. patens* Goldbl.	12
H. comptonii L. Bolus	12	*H. pendula* Goldbl.	12
H. cookii L. Bolus	12, 24, 36	*H. ramosissima* Schltr.	12
H. elegans (Jacq.) Sweet	12	*H. schlechteri* L. Bolus	12
H. fenestrata Goldbl.	12	*H. spiralis* L. Bolus	12
H. flaccida Sweet	24, 36	*H. tenuis* Schltr.	10, 9
**H. flavescens* Goldbl.	9, 12	*H. tricolor* Lewis	12
**H. fuscomontana* Goldbl.	12	*H. vallisbelli* Goldbl.	12
H. galpinii L. Bolus	24		

cultivation, so are certainly under no threat to their continued existence. Only two species, *H. elegans* and *H. comptonii*, appear exceptions to these observations. Both grow on rich clay soils in the Caledon-Bredasdorp area, and their populations have been severely reduced in size and number by land cultivation. They are probably also adversely affected by the local spraying of weed killers which is occurring on an accelerated scale. *Homeria elegans* is on the point of becoming endangered and in fact now is known from only three small populations, although others probably exist. *Homeria comptonii* is only slightly less threatened, but this species has a wider range and also grows on marginal land not likely ever to be cultivated. Lastly, *H. odorata*, endemic to the Nieuwoudtville area, is potentially endangered over much of its range as it grows mainly on deep clay soil which could at the whim of landowners be ploughed for growing a crop. If such activity occurred, the species would become restricted to a few rocky places surrounding the arable area.

CYTOLOGY

Chromosome cytology of *Homeria* is well known (Goldblatt, 1980a). There is at least one count for every species (Table 4), the first reports for five, *H. bolusae*, *H. patens*, *H. autumnalis H. fuscomontana* and *H. flavescens*, being presented here (Table 5), together with some new counts in other species. Basic number is clearly $x = 6$ and the majority of species are diploid, a few of these with polyploid populations. The basic karyotype comprises large, acrocentric chromosomes ranging in size from 8–5 mμ.

TABLE 5. Locality (all South Africa) and voucher data for original counts in *Homeria* cited in this paper. Chromosome number (diploid) is given for each locality. All collections are housed at MO.

H. autumnalis. Cape Province: Elandskloof, *Goldblatt 5504* (12).
H. bulbillifera subsp. *bulbillifera*. Cape Province: Franskraal, *Goldblatt 5366* (10).
H. cedarmontana, Cape Province: Cedarberg, Middelberg, *Goldblatt 5146* (12).
H. flavescens. Cape Province: Cedarberg, Krom Rivier turnoff, *Goldblatt 4058A* (9). Dwars Rivier, *Goldblatt 4817* (9—previously reported as *H. tenuis* in Goldblatt (1980a)).
H. fuscomontana. Cape Province: Swartruggens, road to Katbakkies, *Goldblatt 5344* (12).
H. bolusiae. Cape Province: Near Bulshoek, Clanwilliam district, *Goldblatt 5660* (12).
H. galpinii. Cape Province: Fernkloof, Hermanus, *Goldblatt 5175* (12).
H. miniata. Cape Province: Krom Rivier farm, *Goldblatt 5124, 5671* (12). Top of Pakhuis Pass, *Goldblatt s.n.* (12). Near Berg River bridge, *Goldblatt s.n.* (12).
H. patens. Cape Province: Flats east of Pakhuis Pass, *Goldblatt s.n., 5159* (12).
H. tenuis. Cape Province: Top of Pakhuis Pass, *Goldblatt 5155* (8). Near Leipoldt's Grave, Pakhuis, *Goldblatt 4805* (9). Elands Kloof, *Goldblatt 5246* (9). Middleberg, Cedarberg, *Goldblatt 5132* (9). Driehoek road, Cedarberg, *Goldblatt 5122, 5674* (10).

Polyploidy is evidently a significant factor in the evolution of the genus. Three species are polyploid: *H. collina* and *H. marlothii* are tetraploid, $2n = 24$; and *H. flaccida* has populations with $2n = 24$ and 36. Three species, *H. bulbillifera, H. britteniae,* and *H. galpinii* have diploid and tetraploid populations, and another, *H. cookii,* has diploid, tetraploid, and hexaploid populations.

Aneuploidy has been found in three species: *H. pallida* has cytotypes with $n = 6$ and $n = 4$; *H. tenuis* has $n = 5$ and $n = 4$ and several populations with $2n = 9$; while *H. flavescens* has $2n = 9$. Cytotypes with $2n = 10$ have one pair of metacentric chromosomes, those with $2n = 9$ have three metacentrics, and those with $2n = 8$ have two pairs of metacentrics. This pattern indicates that the derived karyotypes may have originated through Robertsonian type translocations (Jones, 1977, 1978) as postulated (Goldblatt, 1979a) in the related genus *Galaxia*. Meiosis is regular in the few outcrossing species examined, all $x = 6$ but *H. tenuis,* and the aneuploid cytotypes of *H. pallida* and *H. flavescens* are complex heterozygotes in which the chromosomes form complete rings or chains. Segregation at meiosis is alternate (Goldblatt, 1980b).

RELATIONSHIPS

The relationships of *Homeria* have been rather extensively dealt with in an earlier paper (Goldblatt, 1980a), in which I develop in detail my belief that *Homeria* was derived from *Moraea*-like ancestors. This hypothesis needs only be summarized here. The general morphology of *Homeria,* with its bifacial, channeled leaf and single-internode, apically rooting corm make it clear that the genus is related to *Moraea, Hexaglottis, Galaxia,* and a few other genera which share these same characteristics. This group forms a natural alliance within the Iridaceae-Iridoideae, and has been treated as a subtribe, Homeriinae (Goldblatt, 1971a; emend. 1976a). Within this subtribe I have regarded *Moraea* as the least specialized, and thus most like the ancestor of the group. In *Moraea* the most primitive species have several leaves, unlimited branching, generalized flowers, with

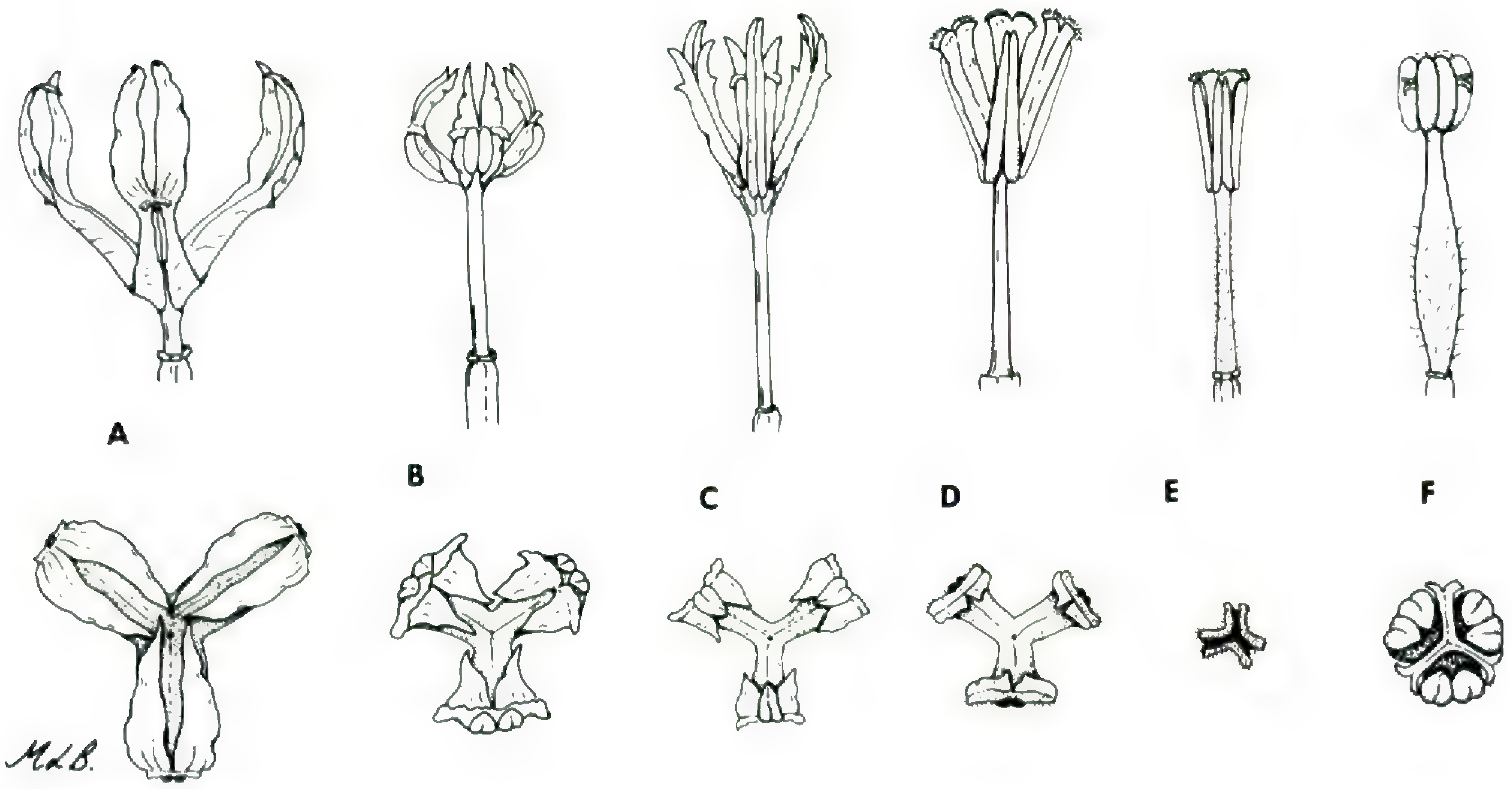

FIGURE 3. Side and top view of the stamens and style branches of *Moraea* and *Homeria*.—A. *Moraea bipartita*.—B. *Homeria schlechteri*.—C. *H. pallida*.—D. *H. ochroleuca*.—E. *H. longistyla*.—F. *H. miniata* (enlarged, but drawn at different scales).

subequal tepals, large petaloid style branches (Fig. 3A) and either free, but contiguous, or basally united filaments, and a basic chromosome number of $x = 10$. Specialization in several lines in *Moraea* has led to a single leaf, limited or no branching, specialized flowers with highly differentiated inner and outer tepals, occasionally a reduction of the petaloid style branches, and progressive decreases in chromosome number, which appears to have stabilized independently in at least two lines at $n = 6$.

In vegetative features *Homeria* is almost identical to *Moraea*, so that it is often impossible to tell them apart. The flower of *Homeria*, however, has an appearance which makes it possible at a glance to recognize it. The tepal claws usually form a cup around the stamen-style branch apparatus, with the limbs of both tepal whorls spreading horizontally. The filaments are usually entirely united (sometimes free near their apex) (Figs. 3B–3F) and the style branches are either narrowed (but with short crests and thus *Moraea*-like in miniature) (Figs. 3B–3C) or reduced to short flat lobes without crests and often obscured by the anthers (Figs. 3D–3F). Basic chromosome number in *Homeria* is $n = 6$.

The *Homeria*-type flower described above has probably evolved at least four times: in the genus *Moraea*, in subgenus *Visciramosa* (*M. elsiae*), and in subgenus *Vieusseuxia* (*M. polyanthos*, *M. speciosa*); in the genus *Rheome*, recently segregated from *Homeria* (Goldblatt, 1980a) and perhaps related to *Moraea* subgenus *Moraea*; and in *Homeria* which, though I believe derived from *Moraea*, forms a distinctive natural assemblage whose immediate ancestors are no longer extant.

EVOLUTION

Within *Homeria* the main trends of evolution are:

1. Reduction in leaf number, several leaves being regarded as primitive. This

pattern is repeated in three lines, sections *Namaquana, Homeria,* and *Conanthera.*

2. Shift in position of the lowermost (or only) leaf from a basal to an above-ground position. This is also repeated in at least three lines, only section *Stipanthera* showing no variation in leaf number or basal insertion. Above-ground insertion is regarded as derived.

3. Union of filaments, which are partially free towards the apex in sections *Namaquana* and *Stipanthera* (except forms of *H. cookii*) and entirely united in sections *Homeria* and *Conanthera,* except for forms of *H. flavescens* in which the free parts of the filaments may be a regression to an ancestral condition.

4. Reduction of the style branches and crests. Well-developed and flat, diverging style branches with distinct crests are typical of sections *Namaquana* and *Stipanthera* and of many species of section *Homeria.* Within the latter section there are two trends in the reduction of the style branches. One involves supression of branching, which typically occurs at the anther base, but in *H. minor* is towards the midline of the anthers, and in *H. longistyla,* the style divides at the anther apex or beyond, or may not branch at all. A second trend is for the branches to shorten, and become bilobed, while the crests are suppressed (*H. vallisbelli*).

In section *Conanthera* the style branches are always short, and bilobed, and lack crests. The anthers instead of diverging are contiguous, and conceal the style branches, only the apices of which emerge between or above the anthers.

Among the criteria listed section *Namaquana* stands out as most unspecialized, while the three other sections appear to have diverged early from basal stock, along different lines. Each of these has a mixture of derived and primitive features. Sections *Homeria* and *Conanthera* exhibit a large degree of internal specialization with rather similar end points achieved by convergence of vegetative and floral characters in the most specialized species of each.

SUBGENERIC CLASSIFICATION

It seems useful to provide a subgeneric classification for *Homeria,* giving formal recognition to the main morphological groupings. I am accordingly establishing four sections (Table 1).

1. Section **Namaquana** Goldbl., sect. nov.

Folia plures vel solitaria. Tepala unguiculata vel non. Filamenta libera in parte superiore; antherae arcuatae. Rami styli divergentes, arcuati, cristae productae.

Leaves several or solitary in *H. bolusiae.* Outer spathe sheathing but free distally in *H. ramosissima.* Tepals not clawed or with short claws appressed to the filament column. Filaments free in the upper part; anthers arched outwards. Style branches well developed, arched, the broad stigma appressed to the anther and stigmatic laterally, the crests well developed, horizontal. Chromosome number $2n = 12$.

Type species: *H. schlechteri* L. Bolus.

The section comprises three species which occur along the west coast from

near Clanwilliam to the Springbok area of Namaqualand. Distribution of the species is complementary. All are diploid. The many leaves, unrestricted branching, apically free filaments and well-developed style branches mark section *Namaquana* as primitive in the genus. The stellate flowers in *H. schlechteri,* the tepals of which lack claws, are probably derived, the clawed condition presumably being ancestral.

2. Section **Stipanthera** Goldbl., sect. nov.

Folium solitarium, basale. Tepala unguiculata, ungues breves vel longi et cupulati, filamentis inclusis. Filamenta libera in parte superiore vel omnino connata; antherae rectae, divergentes. Rami styli longi, divergentes, cristae distinctae.

Leaf solitary, always basal. Outer spathe sheathing. Tepals clawed, the claws short and appressed to the filament column, or long and enclosing filaments in *H. britteniae*. Filaments usually free in the upper 1–2 mm, but entirely united in some populations of *H. cookii*; anthers straight. Style branches long, narrow, diverging, with distinct short crests. Chromosome numbers $2n = 12, 24, 36, 8$.

Type species: *H. cookii* L. Bolus.

Section *Stipanthera* comprises four species, and includes two wide ranging species *H. cookii* and *H. pallida,* and the more localized *H. marlothii* and *H. britteniae*. The distribution of the section encompasses almost the whole range of the genus, but it does not extend to the extreme southwestern Cape nor into Namaqualand. The ranges of the species are predominantly complementary, with limited sympatry between *H. cookii* and *H. pallida* in the northern karoo.

The section is specialized in having a single leaf, this always basal, but primitive in having apically free filaments and well-developed style branches.

3. Section *Homeria*

Leaves several in *H. cedarmontana,* 2 in *H. ochroleuca,* but typically solitary, either basal or inserted well above ground. Spathes entirely sheathing. Flowers varied; tepals always clawed, the claws usually forming a cup or tube to enclose part or all of the stamens. Filaments entirely united, often papillate or pubescent, but free in the upper part in *H. flavescens*; anthers straight, diverging or parallel. Style branches either well developed, with distinct, short crests, or the crests vestigial to absent, or the branches suppressed in *H. longistyla*. Chromosome numbers $2n = 12, 24, 36, 10, 9, 8$.

Type species: *H. collina* (Thunb.) Salisb.

Section *Homeria* is the largest in the genus, comprising some 15 species. Among these are some of the most striking representatives in the genus, such as the large-flowered *H. elegans* and *H. comptonii* with maculate tepals. Species range from the many-leafed Cedarberg endemic, *H. cedarmontana,* to the dwarf tiny-flowered *H. tenuis*. Typically species of section *Homeria* have a single leaf, either basal, or inserted well above ground, as in the majority of species. Differences between many species are small and difficult to distinguish in dry material, as they are mainly in the structure and orientation of the tepals and the form of the tepal cup. The filaments are entirely united, except in *H. flavescens,* possibly

a regressive character, although this species may be misplaced here. Section *Homeria* is concentrated in the southwestern Cape, with extension northward to Nieuwoudtville, and eastward to Grahamstown, almost entirely within the Cape Floristic Region. Speciation is marked along the west coast, mainly in the Cedarberg-Cold Bokkeveld ranges where nine species occur in the area between Nieuwoudtville and Gydo Pass, six of which are endemic, including the cytologically interesting ring-forming complex heterozygote populations of *H. flavescens* and *H. tenuis*.

There is a trend in the section for reduction of the style branches, which become fairly short in *H. minor* and are entirely suppressed in some forms of *H. longistyla*. Crests are uniformly small where present, but are difficult to detect in *H. ochroleuca*, lacking in *H. longistyla, H. vallisbelli* and *H. flavescens*. This is accompanied by a tendency for anthers to become parallel, and even coherent, round the style or its branches.

4. Section *Conanthera* Goldbl., sect. nov.

Folia plures vel solitaria, basalia vel supra terram inserta. Tepala unguiculata. Filamenta omnino connata; antherae cohaerentes, ramis styli tectis. Rami styli breves, bifurcati, apices interantheras extensi, cristae deficientes.

Leaves several to solitary, the lowermost basal or inserted above ground in *H. fenestrata* and *H. brachygyne*. Spathes entirely sheathing. Tepals clawed, the claws either short and appressed to the lower part of the filament column, or long, and forming an open cup round the filaments, *H. fenestrata, H. tricolor,* or including the anthers as well, *H. odorata*. Filaments united, the column straight or bulbous at the base; anthers short, parallel, cohering, initially covering the style branches but collapsing after anthesis and the style branch apices extending between or above the anthers. Style branches short, broad, bilobed, lacking crests (or vestigial and obscure). Chromosome numbers $2n = 12(-24)$.

Type species: *H. miniata* (Andr.) Sweet.

Section *Conanthera* includes species with several leaves, *H. miniata, H. pendula, H. spiralis* and *H. fenestrata*, and single leafed-species, *H. bifida, H. odorata, H. brachygyne* and *H. fuscomontana,* while *H. tricolor,* typically solitary leafed, may also have up to three leaves. Species are all small flowered, except the striking Kamiesberg endemic, *H. pendula* which has large, pendant flowers with reflexed tepals. Species of the section share stamen and style branch characters, and are readily recognized by their short coherent anthers, short, broad bilobed style branches, initially hidden by the anthers. After anthesis the anthers collapse and the apices of the style branch lobes are visible either between or beyond the shrunken anthers. The style branches lack visible crests and appear quite flat to the naked eye. There is an interesting specialization in the filament column of *H. miniata, H. pendula* and *H. bifida,* in which the base is enlarged and bulbous.

The section is concentrated in the southwestern karoo and Namaqualand. *H. miniata* is the most widespread, ranging from northern Namaqualand to the Cape Peninsula, and east into the upper karoo. Other species have much more restrict-

ed ranges, with *H. spiralis, H. odorata, H. pendula* and *H. fenestrata* very local in distribution.

Morphology

Corm

The corm is of the single-internode type found in all members of subtribe Homeriinae, in which roots are produced from the lower part of the apical bud which is situated at the top of the corm. The tunics of *Homeria* are distinctive, consisting of very tough black or very dark brown layers perforated at regular intervals. This type of tunic is also found in several species of *Moraea*, notably subgenus *Moraea* sect. *Deserticola* and subgenus *Vieuseuxia* section *Polyanthes*. Corm size varies in the genus from the very large corms of *H. marlothii*, some 35 mm in diameter, to the very small ones of *H. tenuis*, sometimes no more than 5 mm in diameter.

Leaves

The produced leaves are bifacial and of the *Moraea* type (Goldblatt, 1976b), usually linear and channeled. Leaf number varies from several in *H. schlechteri* and *H. ramosissima*, a presumably primitive condition, to few (2–3) in *H. miniata, H. spiralis, H. fenestrata, H. cedarmontana,* and *H. pendula*, to solitary in the majority of species. *Homeria ochroleuca* and *H. tricolor* are unusual in the genus, having populations with solitary or more than one leaf.

Point of insertion of the lowermost (or only leaf) is an important taxonomic character in the genus. Insertion ranges from at or near ground level to well above ground. The character is constant within most species, and shows little variation except in *H. bulbillifera*, which typically has a basal leaf; however, inland populations growing on clay tend to have the leaf inserted somewhat above ground. Position of the leaf insertion is used frequently in the key and in defining species. Within section *Homeria* there is a large natural group of species with above-ground leaf insertion, including *H. flaccida, H. collina, H. minor, H. ochroleuca, H. galpinii, H. tenuis,* and *H. longistyla*. This is characteristic also of *H. fenestrata, H. fuscomontana* and *H. brachygyne*, section *Conanthera*, and *H. bolusiae*, section *Namaquana*.

The produced leaf, or more simply the leaf, is generally quite distinct from other foliar appendages. These are: (1), cataphylls, transparent and membranous structures which sheath the underground part of the stem and emerge only shortly above ground; and (2), entirely sheathing, but herbaceous structures borne above the leaf or leaves, at nodes on the stem. These strongly resemble the spathe valves or bracts which enclose the inflorescences, and are termed stem bracts here. In the less specialized species the stem bracts are not always clearly distinct from the leaves and have a free apical portion. They are thus actually short leaves rather than bracts. *Homeria schlechteri* and *H. ramosissima* are two species where the leaf stem bract distinction is blurred. In *H. minor* the single bract leaf is often rather leaflike, but so much shorter than the produced leaf that *H. minor* is treated as a solitary leafed species.

STEM

Each corm produces only a single stem, which is normally erect or slightly inclined. The stem may be straight, but in species with the leaf inserted above ground, the stem is usually flexed above the node. The branching pattern is also an important characteristic of species. Branches may be held close to the main axis, with the inflorescences diverging outward, e.g., *H. odorata, H. bifida, H. marlothii,* or the branches may diverge, with upright inflorescences, e.g., *H. cookii.* Branches are numerous and very short in species like *H. bifida* and *H. marlothii,* giving plants a characteristic appearance. In other species, branches are fewer, and longer, and often borne on a flexuose stem, e.g., *H. fenestrata* and *H. spiralis.*

INFLORESCENCE

Individual inflorescences are enclosed in paired, opposed sheathing bracts, called spathes. Each inflorescence contains several flowers, produced serially over a two- to three-week or longer period. The outer spathe is usually about half to two-thirds as long as the inner. In several species, apparently unrelated, the inner spathe elongates during flowering to enclose the developing capsules, functioning in some protective role. This condition occurs conspicuously in section *Conanthera* in *H. tricolor* and in section *Homeria* in *H. comptonii, H. elegans, H. minor, H. vallisbelli,* and *H. tenuis.*

FLOWERS

The six tepals are free with those of the outer whorl somewhat larger than the inner. The tepals are divided into a narrow lower part, the claw, and a broader upper part, the limb, and there is a clear angle or knee dividing the claw from the limb. Both inner and outer whorls are identical in orientation. *Homeria schlechteri* is unusual in that its tepals show no division into limb and claw. Here the tepals spread horizontally from the base. The difference between limb and claw is obscure in the two closely related species *H. comptonii* and *H. elegans.*

In several species the tepal claws together form a cup, partly or entirely including the filaments and stamens. The presence and nature of this cup is an important specific characteristic, but is usually difficult to determine in dried plants unless the flowers are pressed with great care. In others, the tepal claws, usually rather short, are erect and held closely against the filament column. A small cell is thus formed between the tepal and filament base which conceals the nectar. This condition is accompanied in several species of section *Conanthera* with a bulbous enlargement of the base of the filament column, as in *H. miniata, H. bifida, H. spiralis,* and *H. pendula.*

Nectar guides are present in most species, and are either deep yellow to orange patches of color, often outlined in dark green, or dense patches of small dark spots, located at the base of the tepal limbs, and sometimes extending down the tepal claws. Some populations of *H. comptonii* lack nectar guides, while in others there are dark green marks on the outer or both tepal whorls, sometimes large enough to fill the middle third of the tepal. *Homeria elegans* also typically has very large dark green markings in the mid to upper third of the outer tepals.

Nectaries are usually confined to a small area at the base of the outer tepals. These are clearly visible in living plants but obscure in dried specimens. *Homeria ochroleuca* is the only exception: it lacks discrete nectaries, but nectar is secreted over a broad central area of the claws of all tepals, a feature apparent only in living flowers by the presence of droplets of nectar.

The length of time flowers last is an important specific character, but one on which little data is available. Flowers of most species last a single day, opening and fading at constant times. Species of section *Namaquana* are unusual in flowering early in the day, the flowers lasting until about 1 P.M. In section *Conanthera*, species such as *H. miniata*, *H. bifida*, and others flower late, the flowers opening after midday and fading in late afternoon. Longer-lasting flowers are found in section *Homeria* in which the flowers of some species such as *H. collina*, *H. ochroleuca*, *H. flaccida*, *H. longistyla*, *H. collina*, and *H. elegans* last two days, fading on the third in all these except *H. longistyla*.

ANDROECIUM

Filaments are united entirely in the majority of species, but are free in the upper 1–2 mm in section *Namaquana* (Fig. 3A) and in *H. pallida* (Fig. 3B), and most populations of *H. cookii* and *H. britteniae* of section *Stipanthera*. The filament column varies in shape from cylindric and smooth or papillate-pubescent below, to tapering from the base to the apex (*H. collina*, *H. elegans*), to bulbous in the lower part in several species of section *Conanthera* (*H. miniata*, *H. spiralis*, *H. pendula*, and *H. bifida*) (Fig. 3F).

Anthers are oblong to linear and appressed to the style branches. Depending on the orientation of the style branches, the anthers may be erect and contiguous to widely diverging. They are usually straight, but if they exceed the style branches they tend to curve inward after anthesis.

GYNOECIUM

There is little variation in the ovary in *Homeria* except in length, which ranges from 5 mm in *H. tenuis* to over 25 mm in *H. flaccida*. The ovary is usually exserted from the spathes, but included in *H. ramosissima*, *H. comptonii*, *H. elegans*, *H. minor*, *H. tenuis*, *H. flavescens*, and often in *H. cookii* and *H. tricolor*.

The slender style, concealed by the filament column, usually divides just near the apex of the column, forming three flat branches. The structure of the branches ranges from fairly broad and petaloid with paired crests extending well above the stigmas to narrow with short vestigial crests, to terete and bilobed and without crests, and is an extremely important taxonomic character in *Homeria*.

The most elaborate style branches are found in section *Namaquana* in which the broadly flattened arcuate branches are topped by long, horizontal crests. The stigma lobe is wide, and held against the base of the crests with only the sides which extend beyond the crests receptive (Fig. 3B). Almost as elaborate are the style branches of *H. cookii* and *H. marlothii* (section *Stipanthera*), but the branches are rather narrower and straight (Fig. 4C). In section *Homeria* the branches are always straight and usually about as wide as the anthers, and the

crests are short, no more than 1–2 mm, (Fig. 3D) or obscure to absent (*H. ochroleuca* and *H. longistyla*). The stigma, often bilobed, is also small. In two specialized species of the section, *H. minor* and *H. longistyla,* (Fig. 3E) the style divides, not at the apex of the filament column, but well above the anther base. In *H. longistyla* the style branches towards the anther apex, and the branches are short, sometimes barely developed (Fig. 21). In section *Conanthera* the style branches are apparently further reduced to small flat bilobed structures (Fig. 3F). Here the ends of the two lobes of each branch are stigmatic and emerge between or above the connate anthers. There is no development of any crest or crestlike structure.

FRUIT

The fruit of *Homeria* is a loculicidal capsule which is generally oblong to linear, and cylindric to slightly 3-lobed in section. Capsules are generally exserted from the spathes and 10–20 mm long. Capsules of *H. collina* and *H. flaccida* are distinctive in their length, between 25 and 55 mm long, and in having a well-developed beak which is ca. 1 mm long and obtuse in *H. collina,* and ca. 2 mm long and acute in *H. flaccida*. The capsules of *H. comptonii* and *H. elegans* are also unusually long, 25–30 mm, and are enclosed in the spathes.

Seeds are brown, angular, and range in size from ca. 1 mm in diameter to 2 mm in large-capsuled species such as *H. cedarmontana*. The angles of the seeds have membranous transparent ridges, which are too poorly developed to be called wings. Apart from size, there is nothing to distinguish the seeds of different species.

SYSTEMATICS

Homeria Ventenat, Dec. Gen. Nov. no. 2, 1808. TYPE SPECIES: *H. collina* (Thunb.) Salisb.

Moraea L. sensu Thunb., Diss. *Moraea* 1787, pro parte.

Plants small to medium, deciduous perennial herbs. *Rootstock* a single internode corm, rooting from the apex, with tunics of tough black (to dark brown) reticulate layers. *Leaves* several to solitary, inserted basally or on the aerial part of the stem, linear, canaliculate, straight, or coiled in the upper part. *Stem* erect, straight, or flexuous, usually branched, sometimes repeatedly smooth, or in one species, papillate, bearing reduced leaves, or sheathing bracts from the upper nodes. *Inflorescences* several flowered, enclosed in paired, opposed herbaceous bracts or spathes, the outer usually ½–⅔ the inner; in some species the inner spathes elongating to enclose developing fruits. *Flowers* usually yellow, pink, or orange, rarely white, with nectar guides at the base of the limbs of both tepal whorls, usually yellow, or large and green in two species; nectaries located at the base of the outer tepals in most species, rarely absent or diffuse on the tepal claws; tepals free, subequal, or the inner slightly smaller, usually divided into limb and claw; limbs horizontal, or reflexed, the claws erect, and pressed to the filaments or forming a narrow to wide cup. *Stamens* opposite the outer tepals; filaments either united entirely around style, or free in the upper 1–2 mm; anthers

pressed against the style branches, erect or diverging, often exceeding the stigmas and curved inward. *Ovary* oblong-linear; style slender, concealed by the filament column, dividing at the apex of the column, rarely above the base of the anthers; *style branches* flattened, either with broad transverse stigmas and paired stylar crests, or bilobed apically, without crests and stigmatic at the ends of the apical lobes. *Fruit* a loculicidal capsule, cylindrical, flat topped, or beaked. *Basic chromosome number* $x = 6$; diploid numbers $2n = 12, 24, 36, 10, 9, 8$.

Number of species: 31.

Distribution: South Africa, eastern and central Namibia (South West Africa), Lesotho and southern Botswana, concentrated in the winter rainfall parts of the southern and western coasts of the Cape Province, and adjacent parts of the karoo.

KEY TO THE SPECIES

1. Produced leaves 2–several.
  2. Flowers with distinct style crests 2–3 cm long and clearly extending beyond the stigmas, and either erect or incurved.
    3. Anthers 2–3 mm long; tepals spreading from the base or the claw appressed to the filament column and the limb outspread; filaments free in the upper 1–2 mm.
      4. Outer inflorescence spathe entirely sheathing; tepals spreading from the base .... 1. *H. schlechteri*
      4′. Outer inflorescence spathe free in the upper part and curving outward; tepal base (claw) appressed to the filament column for ca. 2 mm .... 2. *H. ramosissima*
    3′. Anthers 9–10 mm long; tepals erect in the lower half, forming a cup around the style and stamens; filaments entirely united .... 8. *H. cedarmontana*
  2′. Flowers without distinct style crests (and the style branches often not markedly flattened).
    5. Filament column ± cylindrical; anthers erect or divergent.
      6. Plants to 30 cm tall; tepals 15–24 mm long; anthers 2–3.5 mm long, erect.
        7. Ovary ca. 4 mm long; filament column 6 mm .... 26. *H. fenestrata*
        7′. Ovary 10–12 mm long; filament column 7–9 mm .... 27. *H. tricolor*
      6′. Plants 35–75 cm tall; tepals 30–40 mm long; anthers 4.5–8 mm long, diverging from the base .... 9. *H. ochroleuca*
    5′. Filament column with a bulbous base; anthers ± erect and contiguous, usually concealing the style branches.
      8. Tepals reflexed at maturity; flowers pendulous or secund .... 24. *H. pendula*
      8′. Tepals outspread or slightly cupped; flowers upright.
        9. Leaves to 4 mm wide, channeled below, flat above, spirally coiled in the upper part .... 25. *H. spiralis*
        9′. Leaves 5–10 mm wide, not coiled, channeled throughout .... 23. *H. miniata*

1′. Produced leaf solitary (lowermost bract-leaf occasionally with free apex and ± leaflike).
  10. Filaments free in the upper (0.5–)1–2 mm; anthers always diverging somewhat; style branches flattened, usually with distinct stigma lobe and style crests.
    11. Leaf 2–4 mm wide and inserted well above ground level; stem flexed above the leaf sheath; anthers 3–4 mm long .... 21. *H. flavescens*
    11′. Leaf more than 5 mm wide, often over 20 mm, inserted ± at ground level, and often sheathing the lower half of the stem; stem not flexed above the leaf sheath; anthers (4–)6–10 mm long.
      12. Ovary 10–15 mm long; lower part of tepals erect, 3–6 mm long, appressed to the lower half of the filament column.
        13. Outer tepals 18–25 mm long, 5–9 mm wide; anthers 4–6 mm long .... 6. *H. pallida*
        13′. Outer tepals 29–43 mm long, 14–18 mm wide; anthers 6–10 mm long .... 4. *H. cookii*
      12′. Ovary (15–)18–24 mm long; lower part of tepals erect, 8–9 mm long, forming a narrow cup enclosing the filament column and part of anthers .... 7. *H. britteniae*

10′. Filaments united entirely; anthers diverging or parallel and contiguous; style branches flattened or not, the stigma lobe distinct with crests developed or the stigma and crests obscure.
14. Anthers 2–3(–3.5) mm long; style branches 1–2 mm long.
15. Leaf basal, sometimes sheathing the lower half of the stem; stem not flexed or bent above the leaf sheath.
16. Leaf 4–7 mm wide; ovary 10–12 mm long; plants 10–30 cm tall .... 27. *H. tricolor*
16′. Leaf 10–20 mm wide; ovary 6–9 mm long; plants 20–75 cm tall.
17. Lower part of tepals (claw) ca. 2 mm, appressed to the filament column; filament column bulbous below .... 28. *H. bifida*
17′. Lower part of tepals (claw) ca. 8 mm long, forming a narrow tube enclosing the filaments and anthers; filament column widened below, not bulbous .... 29. *H. odorata*
15′. Leaf inserted well above ground; stem flexed above the leaf sheath.
18. Tepals 16–28 mm long; filament column 5–8 mm long; spathes 3–5 cm long.
19. Tepals 16–22 mm; filament column 6–8 mm long.
20. Tepals pink salmon .... 31. *H. brachygyne*
20′. Tepals yellow .... 30. *H. fuscomontana*
19′. Tepals 25–28 mm; filament column 5–6 mm long .... 3. *H. bolusiae*
18′. Tepals 10–12 mm long; filament column 5–6 mm; spathes 2–4 cm long .... 22. *H. tenuis*
14′. Anthers (3–)4–13 mm long; style branches 3–10 mm long.
21. Anthers 8–13 mm long; style branches flattened, with distinct crests.
22. Tepal claws 4–5 mm long, erect and clasping the filament column.
23. Anthers usually exceeding the stigma lobes; ovary usually partly included, not flexed at the apex of the pedicel and the flower upright .... 4. *H. cookii*
23′. Anthers usually only reaching the base of the stigmas; ovary exserted, flexed at the apex of the pedicel and the flower secund .... 5. *H. marlothii*
22′. Tepal claws ca. 14 mm long, spreading from the base and forming a wide cup or ill-defined and not cupped.
24. Leaf inserted well above ground; ovary partly to entirely exserted; inner spathe not elongating in fruit and capsules fully exserted from the spathes .... 13. *H. flaccida*
24′. Leaf inserted at or shortly above ground level; ovary usually entirely included; inner spathe elongating in fruit, enclosing and always exceeding the capsules.
25. Tepals obpandurate-spatulate, widest in the upper third; filaments 7–8 mm long; anthers 8–13 mm usually not reaching the top of the style branches; ovary 18 mm long .... 11. *H. comptonii*
25′. Tepals oblong-lanceolate, widest in the middle or lower third; filaments 5–6 mm long; anthers 8–10 mm, usually exceeding the style branches; ovary 12–14 mm .... 12. *H. elegans*
21′. Anthers 3–7 mm long; style branches either flattened with or without crests, or style virtually unbranched.
26. Leaf ± basal and stem not flexed above the leaf sheath.
27. Anthers 4.5–7 mm; tepal claws 9–11 mm long, forming a cup around the filaments.
28. Leaf apex not thickened or prominent; stem often bulbilliferous; blooming August–November .... 10. *H. bulbillifera*
28′. Leaf with prominent, thickened flat apical portion; stem never bulbilliferous; blooming April–June .... 14. *H. autumnalis*
27′. Anthers 6–10 mm; tepal claws 4–6 mm long, clasping the filament column, stems never bulbilliferous .... 4. *H. cookii*
26′. Leaf inserted above ground and stem flexed or bent above the leaf sheath.
29. Style dividing at or shortly above the apex of the filament column (below midline of anthers); style branches diverging when flower fully open or ± erect.

30. Filament column (6–)7–10 mm long; style branches diverging widely (sometimes forced together after anthesis by the incurving anthers when the anthers exceed the style branches) or ascending and ± contiguous.
  31. Ovary (12–) 13–19 mm long; capsule 20–40 mm long.
    32. Filament column glabrous; style crests short and obtuse or evidently lacking .... 9. *H. ochroleuca*
    32'. Filament column minutely papillate-puberulous; style crests triangular, 1–2 mm long .... 16. *H. collina*
  31'. Ovary 8–12 mm long; capsule less than 20 mm long.
    33. Style branches diverging, 3–6 mm long with short acute crests; style dividing at the anther base.
      34. Outer tepals 23–35 mm long; anthers 4.5–6 mm long; capsule 17–20 mm long, included or exserted from the spathes .... 10. *H. bulbillifera*
      34'. Outer tepals 25–27 mm long; anthers ca. 4 mm long; capsule 12–15 mm long, included in the spathes .... 19. *H. patens*
    33'. Style branches erect (to slightly diverging, ca. 25 mm long, without crests; style dividing between the base and middle of the anthers .... 20. *H. vallisbelli*
30'. Filament column 4–5(–6) mm long; style branches ascending, ± parallel or slightly diverging, but anthers ± contiguous.
  35. Tepal claws 2–6 mm long, forming a wide to narrow cup including part or all of the filaments only, the anthers well exserted.
    36. Outer tepals 10–12 mm long, the claw 2–4 mm; anthers ca. 2 mm long .... 22. *H. tenuis*
    36'. Outer tepals 16–24 mm long, the claw 5–6 mm; anthers 3–4 mm long .... 21. *H. flavescens*
  35'. Tepal claws 9–15 mm long forming a narrow tubular cup including the filaments and anthers.
    37. Filament column 4–5 mm long; leaf fairly short, seldom over 20 cm long, usually straight, the apex swollen and acute .... 15. *H. galpinii*
    37'. Filament column 6–7 mm long; leaf long, bent and trailing, seldom less than 25 cm long, the apex often dry at flowering .... 16. *H. collina*

29'. Style dividing at or above the midline of the anthers, sometimes not divided; style branches erect.
  38. Ovary usually partly or entirely enclosed in the spathes, the capsules often enclosed; style branches well developed, 2–3 mm long barely reaching or shorter than the apex of the anthers .... 17. *H. minor*
  38'. Ovary usually exserted from the spathes, the capsules exserted; style branches very short, 1–2 mm long or not developed .... 18. *H. longistyla*

1. **Homeria schlechteri** L. Bolus, Fl. Pl. South Africa 8: sub *tab. 306*. 1928. TYPE: South Africa, Cape, Concordia, *Schlechter 11329* (BOL, lectotype; B, E, G, GRA, K, LD, MO, P, PH, PRE, S, US, Z, isolectotypes). South Africa, Okiep, *Pillans 4953* (BOL, syntype).—FIG. 4.

Plants medium to large, 15–30 cm tall. *Corms* to 3 cm in diameter. *Leaves* 3 to several, the lowermost ± basal or inserted shortly above ground, channeled,

FIGURE 4. Morphology and distribution of *Homeria schlechteri*. Habit ×0.5; flower and outer tepal ×1; ovary, stamens and style branches ×3.

8–20 mm wide, the margins straight or slightly undulate, to 35 cm long. *Stem* flexuose, branching from the upper nodes, the main branches also branched, the leaves on the upper nodes often bractlike and 2–5 cm long, with dry apices. *Spathes* 4–6 cm long, the outer one to ⅔ the inner, entirely sheathing, the apices, dry. *Flowers* pale yellow, darker yellow in the center, often edged with grey or green, the tepals spreading from the base, usually twisted through 90°; *outer*

tepals 18–28 mm long, 9–10 mm wide, narrowly obovate, or pandurate, the claw ca. 1 mm long, not clearly distinguished; inner tepals slightly smaller. *Filaments* 4–5 mm long, free in the upper 1–0.5 mm and diverging, the column slender, smooth; *anthers* arched, ca. 2 mm long. *Ovary* 7–10 mm long; *style* branching at the apex of the filament column; *branches* diverging, ca. 2 mm long, flattened, the stigma upright, appressed to the crests, and stigmatic on the lateral, inner surface; crests erect to horizontal, ca. 2 mm long. *Capsule* oblong, 10–13 mm long; *seeds* angular. *Chromosome number* $2n = 12$.

Flowering time: August–September.

Distribution: Namaqualand, from Bitterfontein in the south, to the Springbok area in the north; in flat sandy places; Fig. 4.

Homeria schlechteri is a fairly common species in the Springbok-Okiep copper mining area in northern Namaqualand. Elsewhere it is less frequent. It occurs as far south as the Bitterfontein-Nuwerus area and in the southern part of its range plants are often very slender, with narrow leaves, and few branches, but similar forms have also been recorded near Grootvlei (*Lewis 5740*) and northeast of Springbok (*Maguire 345*). The slender form does not seem to be a geographic race, but it may be an ecotype adapted to peculiar local conditions. Both the typical and slender forms have identical flowers, and there would seem to be no merit in giving taxonomic recognition to the variant. The flowers of *H. schlechteri* last one day, opening early in the morning and fading by 1:00 P.M.

This species is unusual in *Homeria* in having tepals extending outward from the very base, with virtually no distinction between claw and limb. *H. bolusiae*, a local species of the Van Rhynsdorp-Clanwilliam area, shares this flower type, but can easily be recognized by its single leaf and flexed stem. Apart from *H. bolusiae* the only close relative of *H. schlechteri* is *H. ramosissima* which occurs in southern Namaqualand in the Knersvlakte. *Homeria ramosissima* is distinctive in its growth form. The branching pattern produces a rounded inflorescence, and the flowers have a distinct, though short, claw to the tepals which clasp the base of the filament column. *Homeria ramosissima* also has the distal part of the outer inflorescence spathe free and curved outward, a feature which makes it easy to distinguish it from *H. schlechteri* which has entirely sheathing spathes.

SOUTH AFRICA. CAPE: 29.17 (Springbok): Klipfontein (BA), *Wikner s.n.* (SAM-62792-3). Steinkopf, *Salter 3754* (BOL, K). 20 km NE of Springbok (BD), *Barker 6763* (BOL, M, NBG). Okiep (DB), *Pillans 4953* (BOL); *Lewis 5683* (K, NBG); *Dummer s.n.* (K). Hills at Concordia, *Schlechter 11329* (B, BOL, E, G, GRA, K, LD, MO, P, PH, PRE, S, US, Z). 10 mi NE of Springbok, *Lewis 4421* (PRE, SAM). 8 km NE of Springbok, *Barker 8378* (NBG). Near Concordia, *L. Bolus 1383/29* (BOL). Fields at Rooiwinkel, near Okiep, *Goldblatt 2393* (MO).

29.18 (Gamoep): 20 mi NE of Springbok (CA), *Maguire 345* (NBG). 13 km E of Springbok, *Goldblatt 4253* (MO).

30.17 (Hondeklipbaai): Slope near Grootvlei (BB), *Lewis 5470* (BOL).

30.18 (Kamiesberg): 29 km S of Platbakkies, on Kliprand road (BC), *Goldblatt 4054* (K, MO, PRE). 3 km N of Garies (CA), *Goldblatt 3981* (BR, C, MO, PRE, S, WAG). 7 km S of Kliprand (DA), *Hugo 492* (MO, STE).

31.18 (Van Rhynsdorp): Between Bitterfontein and Nuwerus (A), *Lewis s.n.* (BOL).

2. **Homeria ramosissima** Schltr., Bot. Jahrb. Syst. 22: 95. 1900. TYPE: South Africa, Cape, Van Rhynsdorp Div., banks of the Zout R., *Schlechter 8128* (B, lectotype; E, G, GRA, K, MO, P, PRE, US, Z, isolectotypes).—FIG. 5.

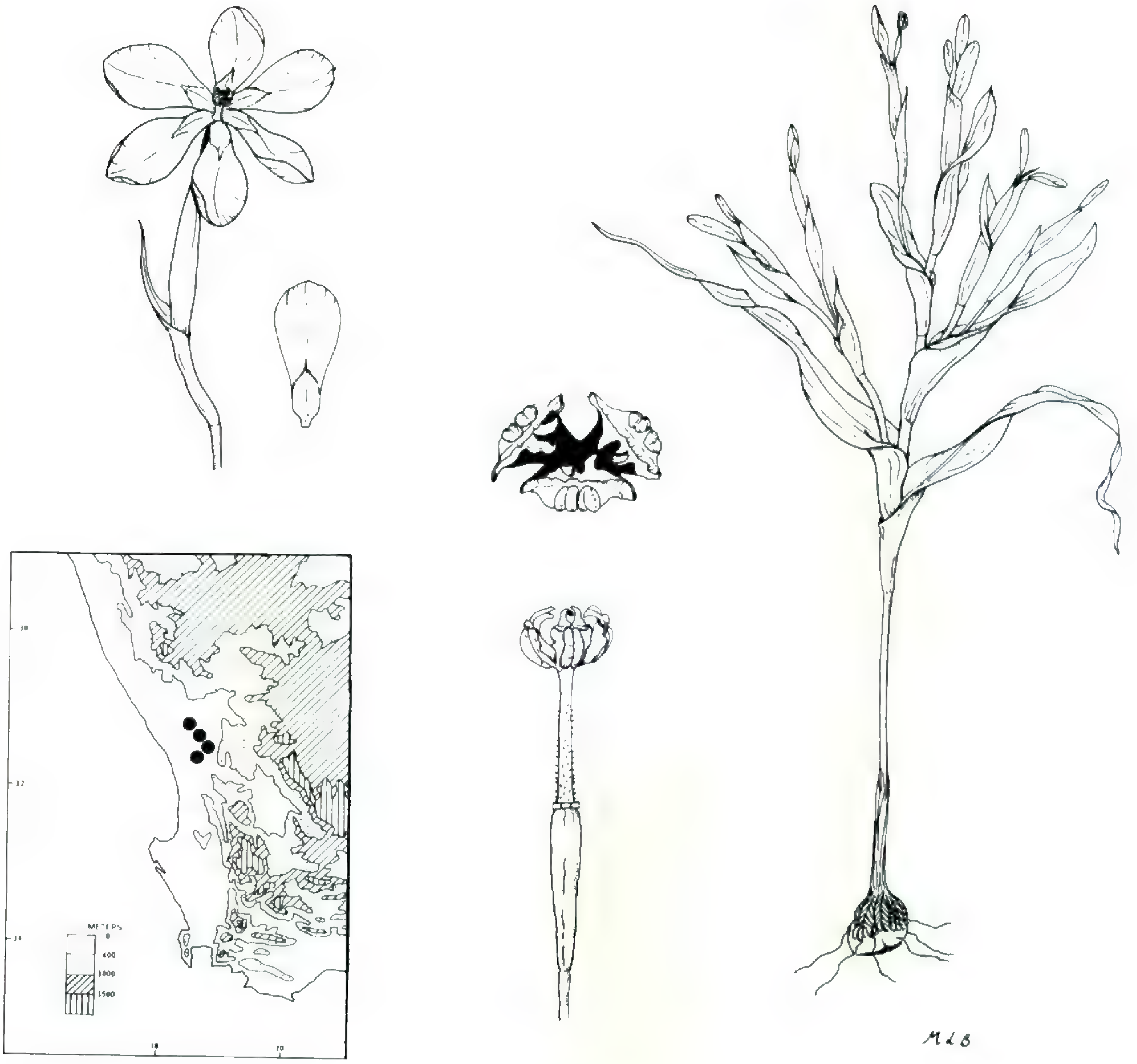

FIGURE 5. Morphology and distribution of *Homeria ramosissima*. Habit ×0.5; flower and outer tepal ×1; ovary, stamens and style branches ×3, the top view much enlarged.

Plants small to medium, 8–20 cm tall. *Corms* 1–2 cm in diameter. *Leaves* several, the lowermost inserted above ground, channeled, somewhat twisted, to 18 mm wide, to 15 cm long, the margins undulate, leaves produced at all nodes. *Stem* erect up to the lower leaf, then flexed above each node, much branched, the branches also branching to form a round head. *Spathes* 3.5–5 cm long, the outer sheathing below with the upper half free and curved outward. *Flowers* pale yellow, with dark yellow in the center, outlined in dark green, the lower part of the tepals held against the filament column for 2 mm, the upper part outspread to slightly reflexed and twisting through 90°; *outer tepals* 17–19 mm long, the claw ca. 2 mm long, the limb narrowly obovate, to 8 mm wide; inner tepals slightly smaller. *Filaments* 6–7 mm long, free in the upper 1 mm and diverging, the column cylindrical, minutely papillate in the lower 2 mm; *anthers* 2–3 mm long, arched. *Ovary* 7–9 mm long; *style* dividing at the apex of the filament column; *branches* flattened, ca. 2 mm long, diverging, the stigma erect, appressed to the base of the crests, receptive on the inner lateral surface; crests ca. 1.5 mm

long, erect, extending above the anthers. *Capsule* ripening while plant still in bloom, oblong-clavate 10-15 mm long. *Chromosome number* $2n = 12$.

Flowering time: late July–early September.
Distribution: Knersvlakte, between Van Rhynsdorp and Nuwerus; Fig. 5.

Homeria ramosissima, with its typical rounded inflorescence is a distinctive plant of the Knersvlakte, the area between Nuwerus and Van Rhynsdorp so rich in succulent plants. It typically has slightly twisted leaves with undulate margins, and outer inflorescence spathes in which the upper part is free and curves outward. Flowers of *H. ramosissima* last a single day, opening early in the morning, and fading by 1:00 P.M. The species is distinctive in its general form, and very unusual for *Homeria* in that every stem axil bears a produced leaf, whereas in other species the upper axils have reduced sheathing bractlike leaves. *Homeria ramosissima* is closely related to *H. schlechteri* but is easily recognized by its overall habit, undulate leaves, absence of stem bracts, inflorescence spathes with apices not sheathing, and clawed tepals clasping the base of the filament column.

SOUTH AFRICA. CAPE: 31.18 (Van Rhynsdorp): Ca. 4 km S of Nuwerus (AB), *Lewis 1632* (SAM). Knersvlakte (B), *Bond 1511* (NBG); *Barker 1313* (NBG); *Compton 20731* (NBG); *Lewis 5532* (NBG); *Esterhuysen 5380* (BOL), *5980* (BOL, K). 33 km N of Van Rhynsdorp (BC), *Goldblatt 3984* (BR, MO, PRE). Zout R., Frames koppie, *L. Bolus s.n.* (BOL-19086). Zout R., *Schlechter 8128* (B, E, G, GRA, K, MO, P, PRE, US, Z). At turnoff to Groot Graafwater, Knersvlakte, *Goldblatt 2550* (MO).

3. **Homeria bolusiae** Goldbl., sp. nov. TYPE: South Africa, Cape, sandstone outcropping near Bulshoek, Olifants R. valley, *Goldblatt 5660* (MO, holotype; K, NBG, PRE, S, WAG, isotypes).—FIG. 6.

Planta 15–40 cm alta. Cormus ca. 10 mm in diametro. Folium unicum, supra terram insertum, 2–4 mm latum. Caulis flexus supra insertionem folii, simplex vel pauciramosa. Spathae 4–5 cm longae, exterior longitudine dimidia ad ⅓ interioris. Flores flavi, unguis brevis, erectis; tepala exteriora ca. 28 mm longa, unguis ca. 1 mm, interiora ad 20 mm longa. Filamenta 5–6 mm longa, connata; antherae 4–5 mm longae divergentes, arcuatae. Ovarium 7–8 mm longum, rami styli lati, ca. 2.5 mm longi, cristae ca. 1 mm longae.

Plants slender, 15–40 cm tall. *Corm* ca. 1 cm in diameter. *Leaf* solitary, inserted well above ground, canaliculate, 2–4 mm wide, longer than the stem, often broken and trailing above. *Stem* erect, flexed above the leaf insertion, usually with a few short branches, the stem bracts 2–4 cm long. *Spathes* 4–5 cm long, the outer ⅓–½ the inner. *Flowers* pale yellow, the tepal claws short, erect, held against the lower part of the filament column, the limbs extended; *outer tepals* ca. 28 mm long, the claw 1–2 mm long, the limb pandurate-obovoid, to 12 mm wide; inner tepals to 20 mm long, 8 mm wide. *Filaments* 5–6 mm long, united, the column slender; *anthers* 4–5 mm long, diverging and arcuate, exceeding the stigmas. *Ovary* 7–8 mm long; *style* dividing at the anther base; *branches* broad, flattened, ca. 2.5 mm long, the stigma upright, held against the crests, receptive on the lateral inner surface; crests ca. 1 mm long. *Capsule* and seeds not known. *Chromosome number* $2n = 12$.

Flowering time: late August–September.
Distribution: Olifants River valley on the slopes of the Nardouw mountains, and north at Lokenberg; Fig. 6.

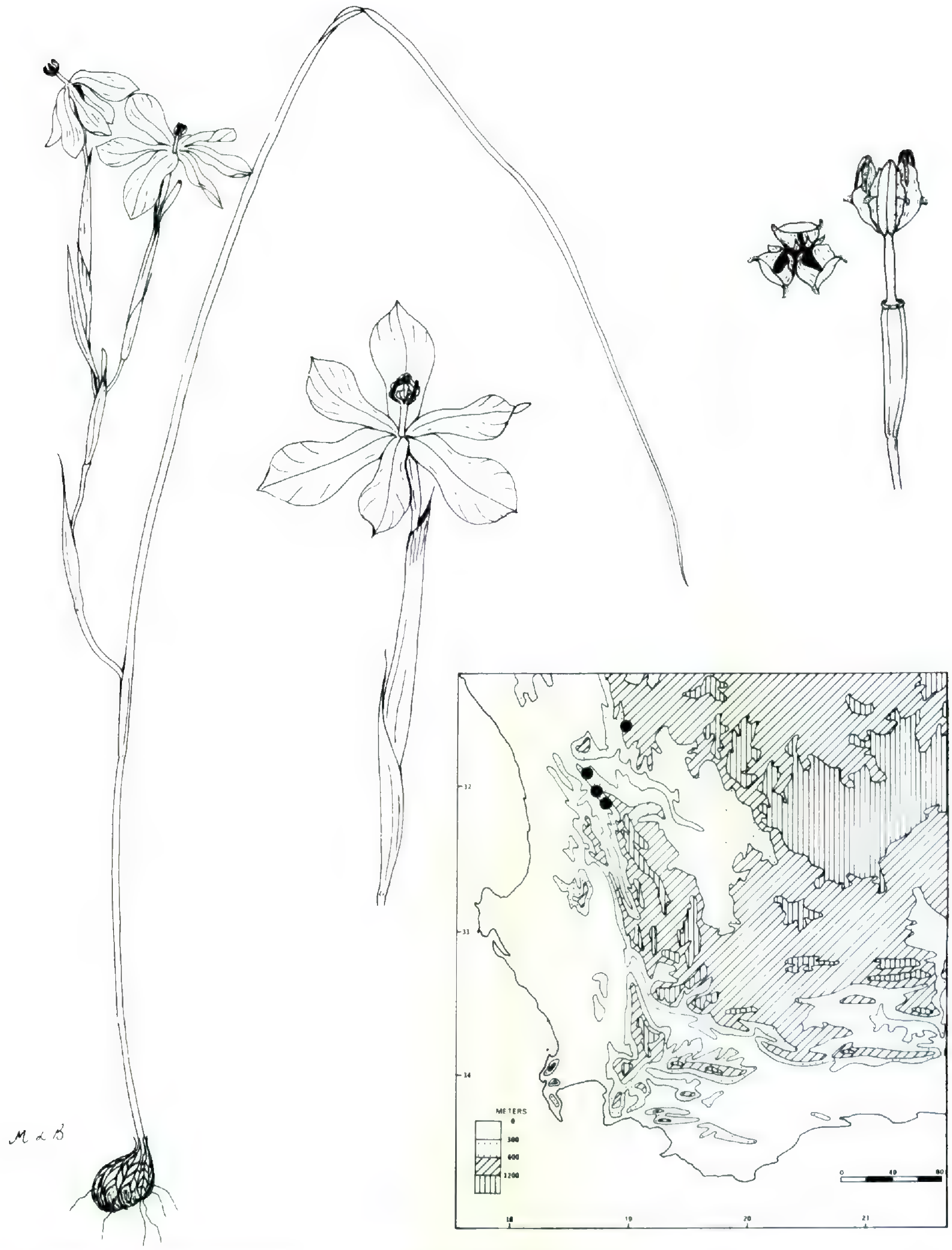

FIGURE 6. Morphology and distribution of *Homeria bolusiae*. Habit ×0.5; flower ×1; ovary, stamens and style branches ×2.

Judging from the very few gatherings, *Homeria bolusiae* may be a rather rare species, but the area between its northern and southern stations is very inaccessible and thus poorly collected, so it may be more common than is indicated. It seems closely related to *H. schlechteri*, a Namaqualand species, and the flowers are almost identical. The flowers of *H. bolusiae* have entirely united filaments,

a filament column 5–6 mm long, and anthers 4–5 mm long, much exceeding the stigma lobe, and shortly clawed tepals. These characters, together with its single rather narrow leaf, set well above ground, and the sharp flexure of the stem above the leaf insertion make *H. bolusiae* easy to distinguish from *H. schlechteri*. Like the other two species of section *Namaquana*, the flowers of *H. bolusiae* open early in the mornings, at first light, and fade between 1 and 2 P.M.

Some confusion may also occur with *H. flavescens* (section *Homeria*) but this species has distinct, long and broad tepal claws, usually shorter filaments ca. 5 mm long, often free near the apex, and anthers usually only 3–4 mm long. Both *H. bolusiae* and *H. flavescens* are poorly known and should be studied further as collections become available.

The species is named in honor of H. M. L. Bolus who made a major contribution to the understanding of *Homeria*. She described some 20 species in the genus in the years 1920–1938, most of them still recognized, thus adding substantially to the total of 6 species admitted by Baker in the *Flora Capensis*, and the 5 more described by Schlechter in 1900.

SOUTH AFRICA. CAPE: 31.18 (Van Rhynsdorp): Nardouw road, on pass (DC), *Barker 7434* (NBG). Sandstone outcropping S of Bulshoek barrage (DD), *Goldblatt 5660* (K, MO, NBG, PRE).
31.19 (Calvinia): Lokenburg (CA), *Acocks 19722* (NBG, PRE), *17023* (K).
31.18 (Clanwilliam): Near Clanwilliam (BB), *Loubser 936* (NBG).

4. Homeria cookii L. Bolus, Fl. Pl. South Africa 8: *tab. 366*. 1928. TYPE: South Africa, Cape, Concordia valley, Montagu Div., *Cook s.n.* (BOL, lectotype; K, isolectotype).—FIG. 7.

H. pillansii L. Bolus, Fl. Pl. South Africa 18: *tab. 684*. 1938. TYPE: S. Africa, Cape, Gydo Pass, *Pillans s.n.* (BOL-19882, holotype; K, PRE, isotypes).

Plants medium to large, (20–)30–60 cm tall. *Corms* 15–30 mm in diameter. *Leaf* solitary, basal, sheathing the lower part of the stem, falcate to trailing above, channeled, (6–)12–25 mm wide, longer than the stem. *Stem* erect, occasionally branching near the base, always from the upper two nodes, the stem bracts usually large (4–)6–9 cm long, the branches short, straight, but flexed below the spathe. *Spathes* (4–)5–9 cm long, the outer slightly shorter than to two-thirds the inner, the inner elongating later to enclose young fruits. *Flowers* pale yellow, occasionally pale salmon, darker towards the center with tiny dark yellow to green spots, faintly scented, the base of the tepals erect, 4–6 mm long, pressed to the filament column, outspread in the upper part, horizontal to slightly reflexed, and often twisted; *outer tepals* 30–43 mm long, the claw 4–6 mm long, triangular, the limb 14–18 mm wide, oblong to slightly obovate; inner tepals 30–35 mm long, 12–14 mm wide. *Filaments* 6–10 mm long, rarely entirely united, usually free in the upper 1–2 mm, the column cylindrical, smooth or sparsely papillate-pubescent in the lower third; *anthers* 6–10 mm long, diverging, the tips curving together. *Ovary* 10–15 mm long, usually included in the spathes; *style* branching at the apex of the filament column; *branches* broad, diverging, 5–7 mm long, curving upwards, the stigma broad, bilobed, stigmatic laterally; crests 2–4 mm long, horizontal. *Capsule* 15–22 mm long, cylindrical to clavate. *Chromosome number* $2n = 12, 24, 36$.

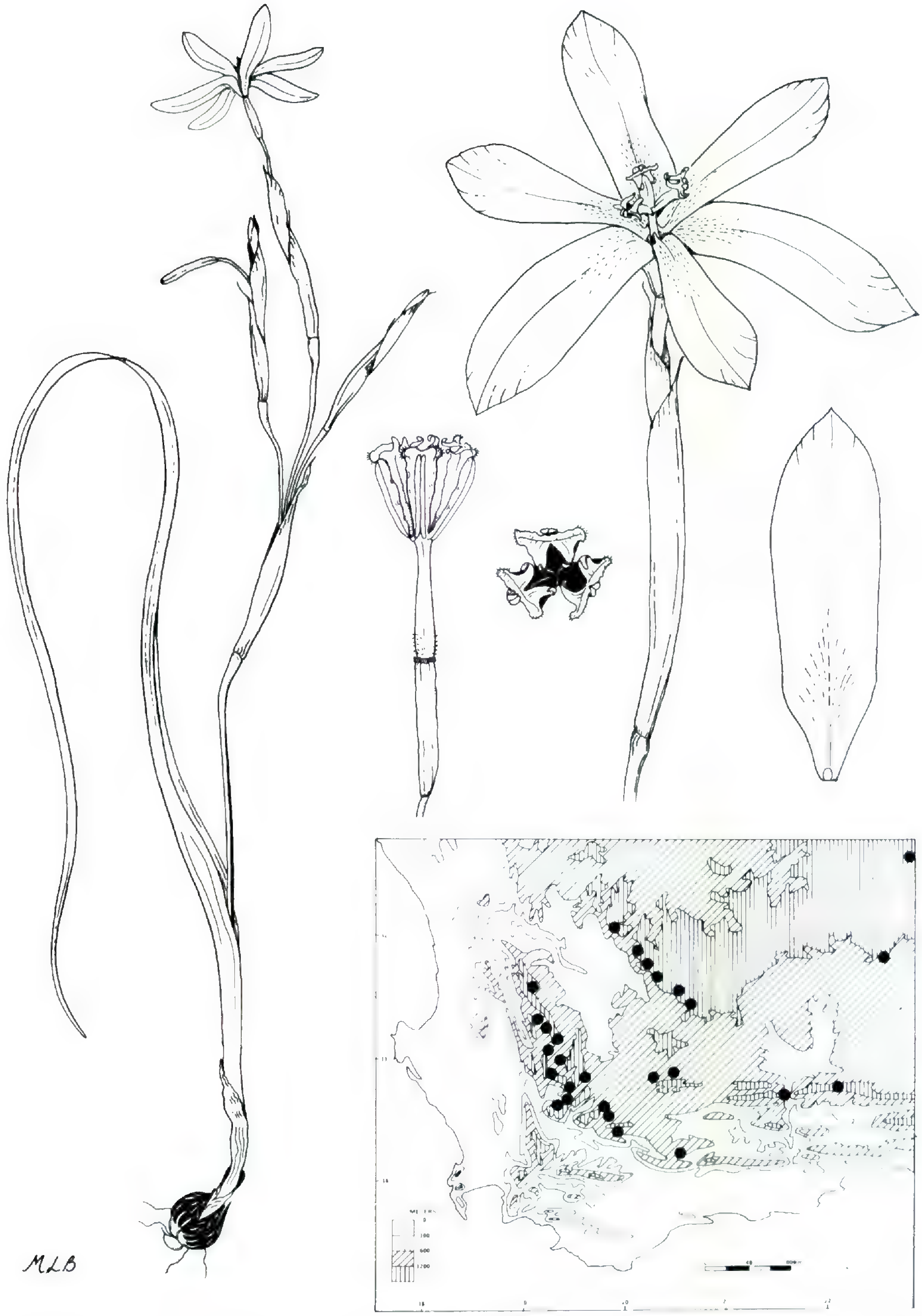

FIGURE 7. Morphology and western part of the range of *Homeria cookii*. Habit ×0.5; flower and outer tepal ×1; ovary, stamens and style branches ×2, the top view much enlarged. The complete range of *H. cookii* is shown in Fig. 9.

Flowering time: late August–October.

Distribution: widespread, mainly at high altitudes, from the Cedarberg in the west, across the Roggeveld mountains and the Swartberg, extending in the east through the karoo at higher elevations to Queenstown, and north in the mountains of the eastern Orange Free State and western Lesotho; Figs. 7, 9.

As circumscribed here, *Homeria cookii* is a very widespread and rather variable species. It extends from the mountains of the western Cape, a winter rainfall area, across the upper karoo to Lesotho, where summer rainfall prevails, but where there is always a certain amount of winter precipitation. *Homeria cookii* thus has a rather unusual distribution, though it is consistent in its occurrence at high altitudes and in its spring blooming. Plants from the western part of its range are usually taller and more robust, and characteristically have the outer inflorescence spathes considerably shorter than the inner. Typically, the western forms have entirely united filaments. The karoo and eastern mountain forms are usually shorter, occasionally quite slender, have narrower leaves, shorter spathes, and always have the filaments free in the upper 1–2 mm. Flower form is fairly constant throughout the range of the species.

Chromosome number is also variable (Goldblatt, 1980a). The two western Cape populations studied are hexaploid, $2n = 36$. A population in the Roggeveld near Sutherland is diploid, $2n = 12$, and the three karoo and eastern populations examined, from Victoria West, Britstown and Sterkstroom are tetraploid, $2n = 24$.

Homeria cookii is related on the one hand to the rather local, western karoo species, *H. marlothii*, and on the other, to the widespread highveld species *H. pallida*. *Homeria marlothii* has a very broad, basal and sheathing leaf, a much-branched stem and occurs in the northern Roggeveld from Middelpos to the Hantam Mountains around Calvinia, always in heavy clay soils. *Homeria cookii* can be distinguished from *H. marlothii* in a general way by a narrower leaf and fewer branches, but more reliably by floral differences. *Homeria cookii* has longer, and relatively narrower tepals with the inner tepals rather smaller than the outer, and flowers always upright. *Homeria marlothii* has smaller, comparatively broader tepals and a much smaller difference between the inner and outer tepals. Its flowers are often secund and always have entirely united filaments.

Relationships between *H. cookii*, especially its eastern form, and *H. pallida* are close. The eastern form is frequently included in *H. pallida*, incorrectly I believe. It is often impossible to distinguish the typical, western form of *H. cookii* from plants found to the east, but easy to recognize differences between the latter and *H. pallida*. The flowers of *H. pallida* are consistently smaller, the tepals seldom longer than 25 mm, and comparatively narrow, while the style branches and crests are shorter than in *H. cookii*, which has tepals in the range of 30–43 mm, and never narrower than 14 mm. There are cytological differences also. All the southern populations of *H. pallida* examined have $2n = 8$ and the northern populations $2n = 12$, compared with three records of tetraploidy, $2n = 24$ in eastern populations of *H. cookii*. *Homeria cookii* and *H. pallida* seem in general to have complementary distribution ranges, with little overlap. Both species have, however, been recorded in the Ficksburg area of the Orange Free State, and near Richmond in the karoo.

LESOTHO. 28.28 (Bethlehem): Leribe (CC), *Dieterlen 187* (K, P, PRE).

29.27 (Maseru): Thaba Tsueu (CD), *Page s.n.* (BOL-17933). Morija (DA), *Jacotet s.n.* (M, Z).

SOUTH AFRICA. CAPE: 29.22 (Prieska): Prieska (DA) *Bryant 843* (K, PRE), *J322* (PRE).

30.22 (Carnarvon): Near Vosburg (DB), *Hafström & Acocks 305* (PRE, S).

30.23 (Britstown): 5 km W of Britstown (DA), *Goldblatt 4680* (MO).

30.25 (Colesberg): Colesberg (CA), *Sidey 1668* (MO, S). Van Schalkwykskraal, Venterstad distr. (D), *Thorne s.n.* (BOL-51962).

31.20 (Williston): Near Blomfontein, W of Middelpos on Calvinia road (CC), *Goldblatt 4273* (MO).

31.23 (Victoria West): Victoria West (AC) *Goldblatt 4681* (MO).

31.24 (Hanover): Naauwpoort (BB), *L. Bolus s.n.* (BOL-14467). Vlakplaas, Richmond, *H. Bolus 13834* (BOL, K), *13897* (BOL).

31.26 (Queenstown): Jamestown (BB), *Barker s.n.* (BOL). Komani R., Queenstown (D), *Galpin 12220* (BOL, K).

32.19 (Wuppertal): Top of Cedarberg Pass (AC), *Goldblatt 4055* (BR, MO, PRE, S, WAG). Top Uitkyk Pass, Cedarberg, *Gillett 4110* (BOL, K, NBG, PRE). Elandskloof (CA), *Martin s.n.* (NBG). Cold Bokkeveld, 45 km E of Citrusdal (CD), *Goldblatt 192* (BOL). Bokkeveld Tafelberg, *Leighton s.n.* (BOL-21506, GRA, PRE). De Keur, *Barker 3108* (NBG).

32.20 (Sutherland): Sutherland road 57 km from Middelpos (AB), *Arnold 937* (PRE). Roggeveld escarpment between Kromberg and Uitkyk (AC), *Thompson 1570* (PRE, STE). Top of Verlaten Kloof (DA) *Marloth 9641* (PRE).

32.22 (Beaufort West): Beaufort West (BC) *Taylor 914* (BOL, K).

32.24 (Graaff Reinet): Graaff Reinet (CA), *H. Bolus 42* (K, S).

32.26 (Fort Beaufort): Whittlesea (BB), *Sim s.n.* (BOL).

33.19 (Worcester): Gydo (AB), *Pillans s.n.* (BOL-19882, K, PRE). *Leipoldt 3017* (BOL, K, PRE), *Leipoldt s.n.* (K). Elandsfontein, 6 mi N of Gydo Pass, *Lewis 2674* (SAM). Groenfontein, Cold Bokkeveld, *Barker 3046* (NBG). Karoopoort (BA), *Barker 1317* (NBG). Near Theronsberg Pass (BC), *Dymond s.n.* (BOL-21235, SAM). Triangle, *Compton 3907* (BOL, NBG). Lakenvlei, *Barker 1318* (NBG). E slopes of Swaarmoed Pass, *Goldblatt 4410* (MO). Matroosberg Station-national road, *Goldblatt 4178* (MO). 12 mi S of Matroosberg, Koo road (DB), *Loubser 2059* (NBG).

33.20 (Montagu): Tweedside (AB), *Lewis s.n.* (BOL). Op-de-Tradouw, W of Barrydale (DC), *Goldblatt 4186* (MO, WAG).

33.21 (Ladismith): Seven Weeks Poort (AD), *Phillips 1529* (SAM); *Lewis s.n.* (BOL-31588).

33.22 (Oudtshoorn): Swartberg Mts., on Die Hell road (AC), *Goldblatt 2938* (K, NBG, MO, PRE).

33.23 (Willowmore): Avontuur (CA), *Gillett 1583* (STE). Avontuur, near station, *Fourcade 4268* (BOL, STE).

33.25 (Port Elizabeth): Longmore Forest Station (CC), *Long 1041* (GRA, K, PRE).

Precise locality unknown: Elandshoek, Aliwal N., *F. Bolus 129* (BOL). Concordia valley, Montagu, *Cook s.n.* (BOL, K). Klein Roggeveld, *Marloth 9590* (PRE).

5. **Homeria marlothii** L. Bolus, S. African Gard. 19: 320. 1929. TYPE: South Africa, Cape, Hantam Mts., *Marloth 12787* (BOL, lectotype; K, PRE, isolectotypes).—FIG. 8.

Plants large, 50–75 cm tall. *Corms* large, ca. 35 mm in diameter. *Leaf* solitary, basal, sheathing the lower part of the stem, channeled, 15–35 mm wide, falcate to trailing. *Stem* straight, much branched from the upper nodes, the branches erect, flexed below the spathes, the stem bracts 8–12 cm long. *Spathes* 5–7 cm long, the apices attenuate, dark brown, the outer spathe slightly shorter than the inner. *Flowers* often secund, pale yellow or pink with a nectar guide of dark color near the center, covered with tiny green dots, the lower part of the tepals erect and appressed to the filament column, the upper part spreading horizontally; *outer tepals* 27–34 mm long, the claw to 4 mm long, erect, the limb spreading, 11–17 mm wide, oval; inner tepals slightly smaller, obovate, tapering towards the base. *Filaments* united, the column 7–10 mm long, pubescent in the lower half, cylindrical or slightly bulbous in the lower half; *anthers* 8–11 mm long, diverging,

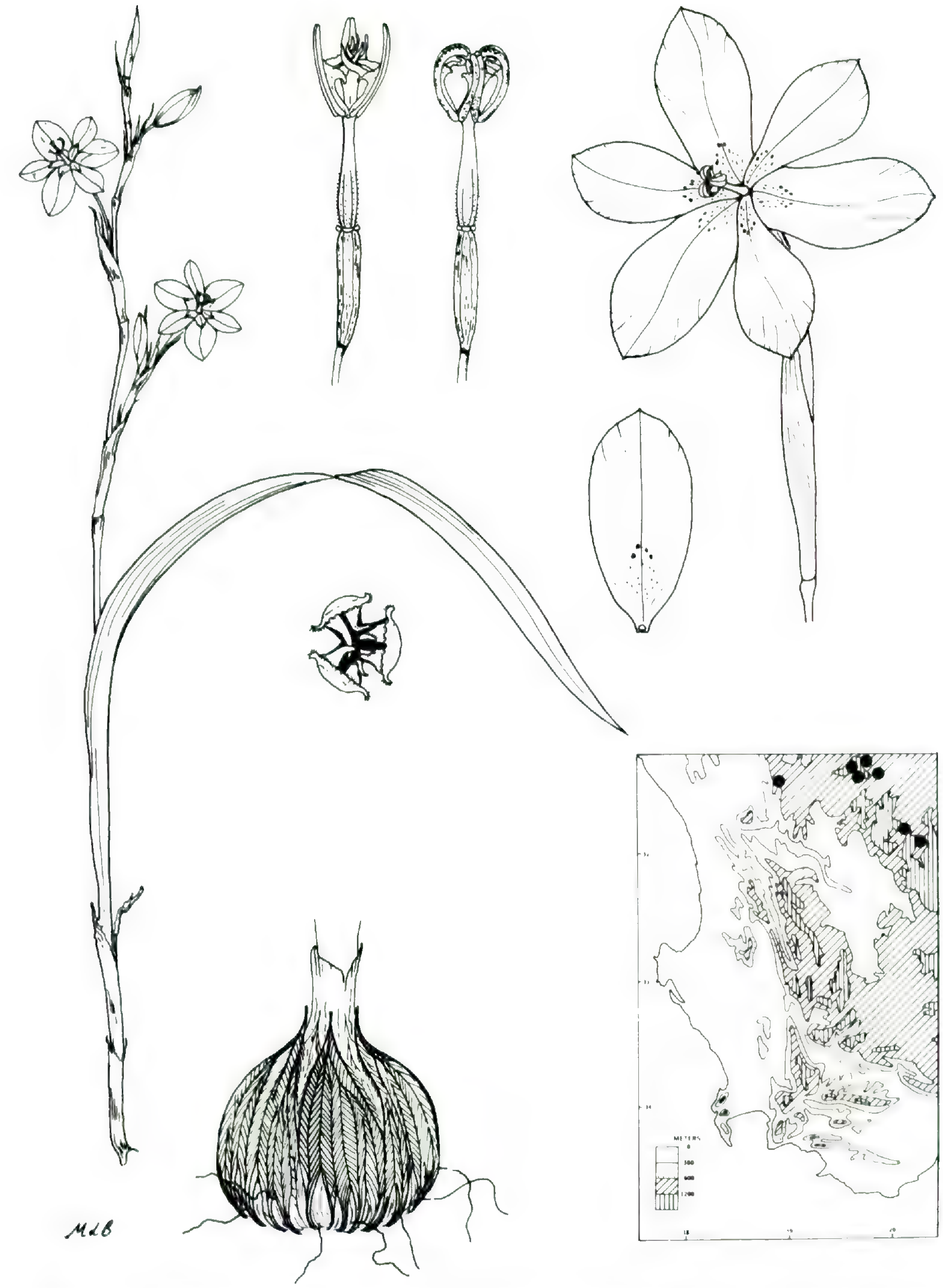

FIGURE 8. Morphology and distribution of *Homeria marlothii*. Habit ×0.5; flower, outer tepal and corm ca. ×1; ovary, stamens and style branches (before and after anthesis) ×1.5, the top view much enlarged.

arched with the apices curved toward the center. *Ovary* 10–20 mm long; *style* branching at the anther base; *branches* diverging, 4–10 mm long, the stigma lobe broad, fertile laterally; crests horizontal, 3 mm long. *Capsule* 2–2.5 cm long, clavate-cylindrical; seeds angled. *Chromosome number* $2n = 24$.

Flowering time: late July–early October.

Distribution: upper Roggeveld between Middelpos and the Hantam mountains, north of Calvinia, and extending east to Nieuwoudtville; usually in rocky sites, in heavy red clay; Fig. 8.

Homeria marlothii is one of the tallest, most robust species of the genus. It has a relatively restricted range in the northwestern Cape in the northern Roggeveld and in the Hantam Mountains. Its closest relative is probably *H. cookii*, a widespread species that occurs to the south in the Roggeveld extending eastwards as far as Lesotho. The two are sometimes difficult to distinguish as they are very similar in habit, though *H. marlothii* has smaller and usually secund flowers. Its tepals range from 27–34 mm long and 11–17 mm wide, with relatively little difference between the inner and outer whorls; also, it always has completely joined filaments. Because of its size and profuse flowering, *H. marlothii* is well worth horticultural attention.

SOUTH AFRICA. CAPE: 31.19 (Calvinia): Uitkomst farm, SW of Nieuwoudtville (AC), *Barker 10737* (NBG). Tierhoek Nek (BC), *Lewis 4804* (SAM). 28 mi N of Calvinia (BD), *Johnson 574* (NBG). 22 mi N of Calvinia, *Maguire 1977* (BOL, NBG). 26 mi N of Calvinia, *Middlemost 1779* (NBG). Moordenaarspoort, N of Calvinia, *Lewis 2556* (SAM), *2557* (SAM). Klipwerf road 34 km N of Calvinia, *Goldblatt 4284* (MO, S), *4285* (K, MO, PRE). Hantamsberg, N of Calvinia, *Marloth 12787* (cult.) (BOL, K, PRE); *Lewis 2588* (SAM); *Goldblatt 681* (BOL); *Acocks 18516* (K, MO, PRE, S).
31.20 (Williston): 24 km NW of Middelpos, near Onderplaas (CC), *Goldblatt 4263* (BR, K, MO, PRE, S). Elandsfontein, Calvinia-Middelpos (DD), *Hutchinson 721* (BOL, GRA, K, PRE).

6. **Homeria pallida** Baker, Handb. Irid. 75. 1892. TYPE: South Africa, Cape, Moshowa R., near Old Litakun, *Burchell 2252-1* (K, lectotype). South Africa, Transvaal, *Holub. s.n.* (syntype not seen).—FIG. 9.

Moraea glauca Wood & Evans, J. Bot. 35: 352. 1897. TYPE: South Africa, Natal, Mooi River, *Wood 4035* (K, lectotype).
Homeria glauca (Wood & Evans) N. E. Brown, Trans. Roy. Soc. S. Africa 17: 350. 1929.
H. humilis N. E. Brown, Trans. Roy. Soc. S. Africa 17: 351. TYPE: South Africa, Transvaal, Pretoria district, *Mare s.n.* (K, lectotype; PRE, isolectotype).
H. mossii N. E. Brown, Trans. Roy. Soc. S. Africa 17: 351. TYPE: South Africa, Transvaal, Geduld, *Moss 15606* (K, lectotype; PRE, isolectotype).
H. pura N. E. Brown, Trans. Roy. Soc. S. Africa 17: 351. TYPE: South Africa, Orange Free State, Parys, *Young s.n. sub Moss 13494* (PRE, lectotype).
H. townsendiae N. E. Brown, Trans. Roy. Soc. S. Africa 17: 351. TYPE: South Africa, Transvaal, Ermelo, *Townsend s.n. sub Moss 15810* (K, lectotype; PRE, isolectotype).
Moraea hakosensis Dinter ex Sölch, Beitr. Fl. Sudwest-Afr., Diss. Univ. München 135. 1960, nom. nud.

Plants medium in size, but from 10–40 cm, slender to robust. *Corms* 1–2 cm in diameter, with black reticulate tunics. *Leaf* solitary, basal, often enveloping the lower part of the stem, and falcate, or erect, with the upper part often bent, and trailing, canaliculate, usually 5–15 mm wide, much longer than the stem. *Stem* erect, sometimes weakly flexed below the nodes, the branches several, straight, flexed below the spathe. *Spathes* 3.5–5(–6) cm long, the inner slightly shorter. *Flowers* yellow, occasionally pink, with dark yellow in the center and green-speckled nectar guides, the lower part of the tepals 3 mm, erect and appressed to the filament column, the upper part of the tepals spread horizontally; *outer tepals* 18–24(–27) mm long, the claw short, narrow, 3 mm long, the limb

5–8(–12) mm wide, ± oblong, occasionally slightly wider in the upper third or near the base; inner tepals smaller, narrowly obovate, to 6 mm wide. *Filaments* partly united, 5–7 mm long, free in the upper 1.5–2 mm, and diverging, the column smooth, cylindrical; *anthers* straight, becoming arched after anthesis, 4–6 mm long, exceeding the stigmas. *Ovary* ca. 10 mm; *style* branching at the apex of the filament column; *branches* diverging, 5–6 mm long, ca. 1 mm wide, the stigma bilobed; crests ca. 1 mm long, erect or curved inward to horizontal. *Capsule* 1–2 cm long, oblong; seeds angled. *Chromosome number* $2n = 12, 8$.

Flowering time: late August–October (rarely until December).

Distribution: widespread from central Namibia (Windhoek) across the northern Cape, southeastern Botswana, throughout the Orange Free State and adjacent Karoo to the south, in the southern Transvaal as far east as Machadodorp and Lydenburg, and in the Natal midlands as far south as Lions River; Fig. 9.

There is an unusually large number of synonyms for *Homeria pallida*, although all but *H. glauca*, in fact, probably represent very little variation. Brown (1929) recognized six species of *Homeria* in the Transvaal and Natal, distinguishing them on what I consider trivial characters such as might be found in the variation pattern of single populations. Flowers of all Brown's species are essentially identical, except for very small size differences, but vegetative form does differ, either in height, number of branches, leaf width, and spathe length. With considerably more material of this small-flowered Transvaal, Natal and Orange Free State *Homeria* now available, it seems likely that there is only one species involved. The single significant variant is the eastern Transvaal-Natal Midlands-Drakensberg foothills form, called *H. glauca*, which differs consistently in having numerous cormlets borne at the corm base, in the axil of the leaf, and sometimes of the lower stem bracts. The flowers are identical with those of *H. pallida*. There seems no good reason to recognize *H. glauca*, despite its unusual cormiferous habit. It seems in all other features like *H. pallida* and evidently occupies the same ecological niche. Significantly not all the Natal collections of the species have the cormiferous characteristic (e.g., *Wright 16*, Lions River).

Homeria pallida is widespread, occurring in a belt across southern Africa in highveld grassland, and it extends from Windhoek (Namibia) in the west to Machadodorp and Lydenburg (Transvaal) in the east. It flowers in the spring, at the end of the long, usually dry winter, before the onset of the summer rainfall season. In areas of complete winter drought, in the southern Transvaal for example, it often occurs in vleis, or similar wet areas, but in the Orange Free State, which may receive some winter precipitation, it grows in open grassveld, where it is very common. *Homeria pallida* is extremely toxic to stock and is the cause of considerable debilitation and death among sheep and cattle.

Cytologically the species is unusual in being heteroploid. Three Transvaal populations examined have the common diploid number of $2n = 12$. Several other populations, all from the Orange Free State, are aneuploid with $2n = 8$, and at least the two populations examined meiotically are complex heterozygotes (Goldblatt, 1980b). The amount of chromosome material in the two cytotypes is the same. The $2n = 12$ form has solely acrocentric chromosomes, and the $2n = 8$

FIGURE 9. Morphology and distribution of *Homeria pallida*. Whole plant including flower ca. ×1; stamens and style branches ×3. Distribution of the related *H. cookii* is outlined.

form two pairs of metacentrics. There are no apparent morphological differences between the cytotypes.

Homeria pallida is related to *H. cookii,* which occurs to the south, from Lesotho, across the southern upper karoo, to the western Cape mountains. The differences between the two species are mainly of size, and the basic vegetative form and floral structure is almost identical. *Homeria pallida* can easily be distinguished by its flowers, the tepals of which are 17 to 25 mm long and up to 8

mm wide, while even the smallest forms of *H. cookii* have tepals longer than 28 mm and 14–18 mm wide.

BOTSWANA. 24.25 (Gaborone): Gaborones Dam (DB), *Lambrecht 324* (K). Content farm (DD), *Hanson 3153* (PRE).

24.26 (Mochudi): Mochudi (AC), *Rogers 6229* (Z).

25.25 (Mafeking): Lobatse-Ghansi (B), *Lambrecht 288* (PRE).

LESOTHO. 29.27 (Maseru): Maseru (AD), *Williamson* 9 (K). Mamathes (BB), *Jacot Guillarmod 2157* (K, PRE). Maseru-Roma (BC), *Gillett 17484* (K, M, MO, PRE). Roma University Campus, *Schmitz 25,8365* (PRE). Morija (DA), *Gilliland s.n.* (J-24998).

NAMIBIA. 22.17 (Windhoek): Frauenstein, near Omuramba (AD), *Giess 13588* (K, M, MO, PRE). Finkenstein, Windhoek Bergland (CB), *Seydel 3640* (G, K, LD, MO, PRE, US).

22.18 (Gobabis): Omatetwa Noord farm (AA), *Homaun s.n. sub Giess 10187* (STE, PRE).

23.16 (Nauchas): Hakosgebirge (A), *Rusch 7959* (B, BOL, K, PRE, Z).

27.18 (Grünau): Grundorn am Gansberg, *Rusch 7922* (B).

SOUTH AFRICA. CAPE: 26.24 (Vryburg): Taungs (CA), *Pole-Evans s.n.* (PRE-15837). Armoedsvlakte, Vryburg (DC) *Henrici 20* (PRE).

27.22 (Olifantshoek): Sishen (DD), *Collins 77* (J).

27.23 (Kuruman): Moshawa R., near Old Litakun (BB), *Burchell 2252-1* (K). Gathlose Bantu Reserve (CD), *McDonald 77/149* (PRE).

28.23 (Griekwastad): Grootfontein (AC), *Wilman s.n.* (BOL). Danielskuil, townlands (BA), *Collins s.n.* (J-42176). W of Griquatown (CC), *Mauve 4140* (J, K, M, PRE).

28.24 (Kimberley): Paardeberg (CC), *Harris s.n.* (BOL-18757). Dronfield (DB), *Badenhorst 22* (K, PRE). Kimberley, *Swanson s.n.* (BOL); *Verdoorn 586* (PRE-35863). Wolwefontein, Barkly West (DA), *Acocks 722* (PRE).

29.22 (Prieska): Prieska (DA), *Bryant 843* (K).

29.23 (Douglas): S bank at junction of Orange and Vaal (BA), *Anderson 678* (BOL).

29.24 (Hopetown): Modder River Station (BA), *Harris s.n.* (BOL-31595, NBG).

30.24 (De Aar): Philipstown (AD), *Vahrmeijer 1374* (PRE).

31.24 (Hanover): Vlakplaats, Richmond Div. (BB), *H. Bolus s.n.* (BOL-13033, PRE).

31.25 (Steynsburg): Reeds farm, Steynsburg (BD), *Pole-Evans 1736* (PRE). Middeburg, *Theron 39* (PRE).

NATAL: 28.29 (Harrismith): Kruisfontein, Bergville dist. (CB), *Nel 2825* (PRE). Cathedral Peak Hotel (CC), *Schelpe 885* (NU).

28.30 (Dundee): Dundee and Glencoe townlands (AA), *Shirley 92* (NU).

29.29 (Underberg): Giants Castle Game Reserve (A/B), *Trauseld 997* (NU, PRE). Giants Castle, along river (BB), *Strey 6992* (PRE). Estcourt, *West 377* (PRE). Heronvale (DB), *Bryant 1277* (PRE).

29.30 (Pietermaritzburg): Mooi River (AA), *Wood 4035* (K). Drayton, Lions R. dist. (AC), *Wright 1560* (E, NU).

30.30 (Port Shepstone): Ixopo (AA), *State Veterinarian s.n.* (PRE-35803).

ORANGE FREE STATE: 26.27 (Potchefstroom): Parys (CD), *Rogers 2944* (PRE), *Smith 6280* (PRE).

27.26 (Odendaalsrus): Odendaalsrus roadsides (BC), *Vahrmeijer 3204* (PRE).

27.27 (Kroonstad): Kroonstad (CA), *Pont 466* (Z).

28.25 (Boshof): Dealesville-Bloemfontein (DB), *Goldblatt 4678* (MO).

28.26 (Brandfort): Virginia (BB), *Goldblatt 4677* (MO). Harmony, *Goldblatt 3412* (MO). N of Brandfort (CB), *Goldblatt 4679* (MO).

28.27 (Senekal): Senekal (CB), *DeWinter 8968* (K, PRE). Schuttes Draai, Ficksburg dist. (D), *Ross 1344* (NU). Ficksburg (DD), *Fawkes 5* (NBG).

28.28 (Bethlehem): Near Kestell (BC), *Strey 9074* (K, MO, PRE). Wodehouse, Buffelsfontein, *Stratton s.n.* (PRE).

28.29 (Harrismith): Rensburgskop, Swinburne (AC) *Jacobz 102* (PRE).

29.25 (Jagersfontein): Spitskop, Fauresmith (CB), *Verdoorn 1580* (PRE). Fauresmith Veld Reserve, *Henrici 1827* (PRE); *Smith 441* (PRE), *912* (PRE). Edenburg (DB), *Pole-Evans & Smith 1824* (PRE); *Smith 546A* (PRE).

29.26 (Bloemfontein): Bloemfontein (AA), *Kriel s.n.* (NBG); *Page s.n.* (BOL-17932); *Potts 2076* (BOL); *Gemmel s.n.* (PRE).

30.25 (Colesberg): Near Springfontein (BC), *Rogers 12122* (BOL); *Thode 5294* (STE).

30.26 (Aliwal North): "Trans Garipina," Nieuwejaarspruit, between Garip (Orange) and Caledon Rivers, foot of the Witbergen (DB), *Ecklon & Zeyher s.n.* (*114.10*) (S).

30.27 (Lady Grey): Zastron (AC), *DeKlerk 2* (PRE).

TRANSVAAL: 24.27 (Thabazimbi): Zyferkraal farm, Nylstroom distr. (BC), *Galpin M662* (PRE).

Zwagershoek, Nylstroom, *Rankin s.n.* (PRE-2754).

24.28 (Nylstroom): Rietvlei farm, Nylstroom distr. (CB), *Burtt-Davy 2359* (PRE). Boekenhoutfontein, Naboomspruit distr. (DA), *Burger 471* (PRE).

24.30 (Pilgrims Rest): Ohrigstad Nature Reserve (DC), *Jacobsen 2952* (PRE). Pilgrims Rest (DD), *Rogers 14706* (K).

25.27 (Rustenburg): Koedoespoort (BD), *Janse s.n.* (PRE-3012). Marsh at Rustenburg (CA), *Moss 11213* (J). Zwartruggens, Rustenburg, *Sutton 940* (PRE).

25.28 (Pretoria): Rooikop, Elands R. (BA), *Pole-Evans 196* (PRE). "Aapjes R." (CA), *Burke s.n.* (K); *Leendertz s.n.* (PRE). Rietvlei, Pretoria, *Repton 4147* (PRE). Pretoria distr., *Mare s.n.* (K). Swartkops Golf Course, Pretoria (CC), *Killick 1531* (K, PRE). Near Bronkhorstspruit (DC), *Mauve 4118* (K, PRE); *Repton 447* (PRE).

25.30 (Lydenburg): Near Lydenburg (AB), *Wilms 1417* (BM, E, G, K, L, P, PRE). Belfast-Dullstroom (CA), *Balsinhas & Kersberg 2064* (PRE). Near Schoonwater, SE of Lydenburg (CD), *Davidson 3223* (MO).

26.25 (Delareyville): Barberspan Nature Reserve (DA), *Zambatis 694* (PRE).

26.26 (Klerksdorp): Lichtenburg (AA), *Pole-Evans 2281* (PRE). Hakboslaagte, *Kinges 1805* (PRE).

26.27 (Potchefstroom): Goedgedacht, Ventersdorp distr. (AA), *Sutton 755* (MO, PRE). Witpoortjie (BB), *Moss 2898* (J); *Gilliland s.n.* (J-26627, PRE). Klip R., at Discovery, *Lucas s.n.* (J). Near Potchefstroom (CA), *Hafström & Acocks 306* (PRE). Vereeniging (DB), *Moss 17313* (J); *Burtt Davy 5567* (PRE), *4695* (PRE). Visgat, E of Vereeniging *Codd 4469* (PRE).

26.28 (Johannesburg): Craighall, marsh (AA), *Lucas 315* (J); *Goldblatt 29, 34* (J). Langlaagte, *Burtt-Davy 1984* (PRE). Park View Golf Course, *Moss 17311* (J, K). Mountain View, Johannesburg, *Moss 17312* (J). Marsh at Geduld (AB), *Moss 15606* (K). Heidelberg (AD), *Moss 17620* (J). 12.5 mi S of Greylingstad (DB), *Scheepers 1602* (K, PRE, WAG).

26.29 (Bethal): Bethal (AD), *Bosch s.n.* (PRE-35790). Standerton (CD), *Rogers 14800* (K, Z). Ermelo (DB), *Townsend s.n. sub Moss 15810* (K, PRE). Nooitgedacht farm, Emelo, *Henrici 1068, 1700* (PRE).

26.30 (Carolina): Carolina (AA), *Rogers 10500* (Z). Streambanks near Carolina, *Galpin 12220* (BOL, K, PRE). Bankop (CB), *Burtt-Davy 1872* (BOL, K).

27.25 (Bloemhof): 8 mi S of Makwassie (BD), *Van Vuuren 1267* (G, K, PRE). Christiana distr. (CC), *Wolff s.n.* (PRE-35850).

27.29 (Volksrust): Marsh, Volksrust (DB), *Schlechter 3436* (BOL, PRE).

27.30 (Vryheid): Wakkerstroom (AC), *Burtt-Davy 2208* (PRE).

7. Homeria britteniae L. Bolus, J. Bot. 69: 11. 1931. TYPE: South Africa, Cape, Grahamstown, *Britten 2951* (BOL; lectotype; K, isolectotype).—FIG. 10.

Plants medium, 20–45 cm high. *Corms* 10–15 mm in diameter. *Leaf* solitary, basal, often sheathing the lower part of the stem, erect or trailing, longer than the stem, channeled, to 9 mm wide, dark green. *Stem* erect, straight, the branches held close to the axis, occasionally unbranched, slightly flexed below the spathes, the stem bracts 6–8 cm long. *Spathes* initially 6–8 cm long, the inner about one-third longer than outer when young, but usually elongating considerably with age, becoming more than twice as long as the outer, enclosing the capsules. *Flowers* pale yellow to cream or white, the nectar guide deep yellow with green spots in the center, the lower part of the tepals forming a narrow tube round the filament column, the upper part of the tepals outspread, slightly twisted from horizontal; *outer tepals* 26–35 mm long, the claw 8–9 mm long, erect, the limb 8–13 mm wide, narrowly obovate or pandurate, widest in the upper third; inner tepals smaller, 21–35 mm long, 5.5–10 mm wide. *Filaments* 7–8 mm long, free in the upper 0.5–1.5 mm or virtually united entirely, the column cylindrical, smooth; *anthers* 6–7 mm, slightly exceeding the stigmas. *Ovary* (15–)18–24 mm long; *style* branching at the apex of the filament column; *branches* diverging and curved upward, 4–6 mm long, the stigma bilobed, broad, receptive laterally; crests short,

FIGURE 10. Morphology and distribution of *Homeria britteniae*. Habit ×0.5; flower, outer tepal and corm ×1; ovary, stamens and style branches ×1.5, the top view much enlarged.

horizontal, 1–2 mm long. *Capsule* cylindrical, (18–)25–45 mm long. *Chromosome number* $2n$ = 12, 24.

Flowering time: mid September–October.

Distribution: southern Cape from Knysna in the west to Grahamstown in the east; often in damp situations; Fig. 10.

Homeria britteniae is fairly common over its comparatively wide range, from about Knysna in the west to the Albany Division in the east. It most often grows

in sandy soils, usually in low-lying areas that are rather moist in the winter. Though often confused with *H. collina*, *H. cookii*, and other single-leafed species, it is comparatively easy to recognize by its very pale, sometimes white flower, dark green basal leaf, very long ovary, and even longer fruit. The basally inserted leaf and apically free filaments indicate an affinity with the *H. cookii-pallida* group. Its long ovary, usually about 20 mm long, and narrow tepal cup enclosing the filament column set *H. britteniae* apart from these species.

Plants from the eastern end of its range, around Grahamstown, have the shortest ovary, sometimes only 15 mm long, and fruits occasionally no more than 20 mm long, but this is still substantially longer than in the related *H. cookii* or *H. pallida*. Sometimes it is difficult to see whether the upper portion of the filaments is free, especially when flowers are carelessly pressed, and this may make accurate determination difficult. The basal leaf insertion and long ovary should then prevent any misidentification.

SOUTH AFRICA. CAPE: 33.23 (Willowmore): Keurbooms R.-Storms R. (C-D), *Gillett 4582* (BOL, K). Grootrivier Pass-Keurbooms R. (CD), *Goldblatt 4921* (M, MO, PRE, S). Longkloof, near Joubertina (DC), *Goldblatt 4947* (MO, NBG).

33.24 (Steytlerville): Near Gamtoos R., W of Humansdorp (DD), *Cassidy 229* (NBG).

33.25 (Port Elizabeth): Addo bush (BC), *Long 147* (K). Uitenhage distr. (CD), *Mund 18* (SAM), *25* (SAM); *Fries et al. 1160* (LD, S, SAM); *Zeyher s.n.* (K). Uitenhage, *Dahlstrand 555* (GRA, PRE). Port Elizabeth (DC), *Holland s.n.* (BOL-31552); *Cruden 467* (GRA). St. Georges Park, *Drège 295* (GRA). Prince Alfred Park, Port Elizabeth, *Cook s.n.* (BOL-20340, SAM-54104). Walmer, *Paterson 2125* (GRA). Swartkops R., Perseverance, *Rodin 1260* (BOL, K, MO, PRE, US).

33.26 (Grahamstown): Near Alicedale (AC), *Bayliss 8066* (MO). Drostdy, Grahamstown (BC), *Blackbeard s.n.* (BOL-31547); *Archibald 5310* (BOL, K); *Britten 2957* (GRA, and cult. at BOL, K); *Dyer 1645* (GRA, K, PRE). Grahamstown, *Bayliss 7629* (G, MO), *6846* (MO). Grahamstown, museum grounds, *Britten s.n.* (BOL-31546); *Schönland 1593* (PRE). Bathurst-Fish R. road (BD), *Bayliss 6723* (MO). Kap R. valley, *Bayliss 8957* (MO).

34.23 (Knysna): Keurbooms River, above the beach (AB), *Goldblatt 5197* (MO).

34.24 (Humansdorp): Witte Els Bosch (AA), *Fourcade 907* (BOL, GRA, STE). Humansdorp-Jeffreys Bay at Swarts R. (BB), *Fourcade 4005* (K, STE). Humansdorp-Cape St. Francis, *Goldblatt 4927* (MO).

8. Homeria cedarmontana Goldbl., sp. nov. TYPE: South Africa, Cape, Cedarberg, slopes half way up Cedarberg Pass, *Goldblatt 3871* (MO, holotype; K, NBG, PRE, S, US, WAG, isotypes).—FIG. 11.

Planta grandis ad 1 m alta. Cormus ca. 2 cm in diametro. Folia 2–3, inferior basale ad 50 cm longa, canaliculata. Caulis erecta, ramosa. Spathae 6–8 cm longae, exterior brevior. Flores lutei, tepala cupuliformi circa columna filamentorum; tepala exteriora ca. 4 cm longa, interiora breviora. Filamenta connata, 16–20 mm longa, puberula infra; antherae 9–10 mm longae. Rami styli ca. 7 mm longi, lati, cristis erectis 2–3 mm longis.

Plants large, 70–100 cm tall. *Corm* deep seated, between rocks, ca. 2 cm in diameter. *Leaves* 2–3, the lower basal, the others cauline, linear, to 50 cm long, erect, trailing in the upper part, channeled, to 2 cm wide. *Stem* straight, branching from the upper nodes, the branches short, held close to the axis, the stem bracts to 10 cm long. *Spathes* 6–8 cm long, the outer only slightly shorter than the inner. *Flowers* yellow, sweet scented, the tepals forming a narrow cup below, enclosing the filament column, spreading horizontally above; *outer tepals* ca. 4 cm long, the claw ca. 2 cm long, erect, the limb horizontal, flaccid; inner tepals somewhat smaller. *Filaments* entirely united, the column 1.6–2 cm long, included in the cup, puberulous in the lower half; *anthers* 9–10 mm long, arching outwards, often

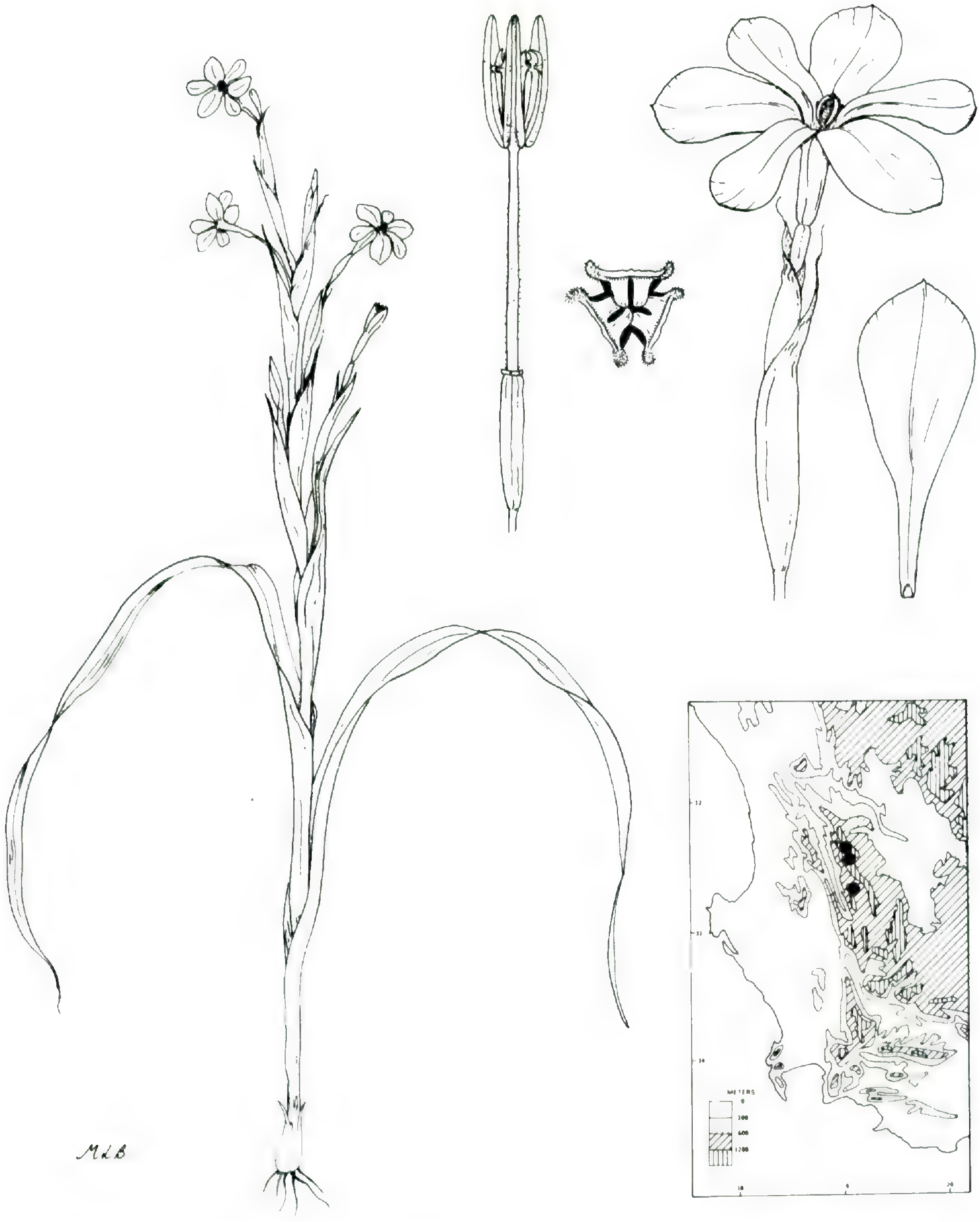

FIGURE 11. Morphology and distribution of *Homeria cedarmontana*. Habit ×0.3; flower and outer tepal ×1; ovary, stamens and style branches ×1.5, the top view ×3.

contiguous at the apices, exserted from the cup. *Ovary* 11–14 mm long; *style* branching at the apex of the filament column; *branches* ca. 7 mm long, diverging, arched upward, the stigma lobe upright, appressed to the base of the crests, the receptive part on the inner lateral surface; crests erect, 2–3 mm long, either exceeding or shorter than the anther apex. *Capsule* clavate-cylindrical, to 2.5 cm long. *Chromosome number* $2n = 12$.

Flowering time: August–October at higher altitudes.

Distribution: local in the Cedarberg; on rocky sandstone slopes; flowering only after fires; Fig. 11.

Homeria cedarmontana is restricted to a limited area of the southern Cedarberg mountains, between Elands Kloof and Middelberg above Algeria. It is seldom seen—though it grows close to roads through Elands Kloof and through the Cedarberg—because it blooms only in the spring following a veld fire. In 1976 when I found the species, it was common and very conspicuous from the mid levels of the Cedarberg Pass and all the way up the Sneeuberg. Hundreds of thousands of plants standing up to 1 meter tall and in full bloom grew on the rocky slopes. The following spring I found hardly a trace of the species in the same area, although a few slender, *Homeria*-like leaves appeared in places. After examining the extensive herbarium collections of *Homeria* I discovered that *H. cedarmontana* had been found twice before, by G. J. Lewis, once in Elands Kloof, and once at Middelberg above Algeria.

Its floral morphology indicates a relationship with the *H. collina* group (section *Homeria*) where its multi-leafed character suggests that it is fairly primitive. It is perhaps close to the line linking section *Homeria* with the generally less specialized section *Stipanthera*.

South Africa. cape: 32.19 (Wuppertal): Sneeuberg, near hut, 1400 m (AC), *Howes s.n. sub Goldblatt 4289* (MO). Slopes of Cedarberg Pass, *Goldblatt 3871* (MO, K, NBG, PRE, S, US, WAG). Middelberg, 4000 ft, *Lewis s.n.* (BOL-31544); *Goldblatt 5146* (MO). Elands Kloof (CC), *Lewis s.n.* (BOL-22065).

9. **Homeria ochroleuca** Salisb., Trans. Hort. Soc. London 1: 308. 1812. type: South Africa, Cape, without locality, illustration in Bot. Mag. *tab. 1103.* 1808 (*H. collina* var. γ) (*tab. 1283* cited in error by Salisbury).—Fig. 12.

Moraea ochroleuca (Salisb.) Drapiez, Dict. Class Nat. Sci. (Encycl. 4. 1832 fide Index Kewensis) 4: 477. 1841.

Homeria collina (Thunb.) Salisb. var. *ochroleuca* Baker, Handb. Irid. 75. 1892 et Fl. Cap. 6: 28. 1896.

H. exaltata Sweet, Hort. Brit., ed. 1: 395. 1826. type: South Africa, Cape, without locality, illustration in Bot. Mag. *tab. 1108* (*H. collina* var γ). 1808.

Moraea exaltata (Sweet) Steud., Nom. Bot., ed. 2, 2: 160. 1840.

Homeria lucasii L. Bolus, S. African Gard. 19: 320. 1929. type: South Africa, Cape, without locality, *Lucas s.n.* (BOL-18572, holotype; K, isotype).

Plants medium to large, 35–75 cm high. *Corms* 1.5–2.5 cm in diameter. *Leaves* 1–3, usually solitary, the lower inserted well above ground level, channeled, longer than the stem, often trailing above, 6–15 mm wide. *Stem* erect, the leaf inserted up to 15 cm above ground, producing 1–several branches from the upper or all nodes, the branches simple, the stem bracts 6–7 cm. *Spathes* (5–)6–8 cm long, the outer about half the inner. *Flowers* yellow entirely, or orange in the center, or occasionally orange entirely, strongly scented, the tepals forming a wide cup, recurved-spreading in the upper half; *outer tepals* 30–40 mm long, the lower part (claw) 13–16 mm long, the nectary area not at the base but diffuse around the middle of the claw, the limb obovate, 15–17 mm wide; inner tepals similar, slightly smaller, also nectiferous. *Filaments* united, the column 7–10 mm

FIGURE 12. Floral morphology and distribution of *Homeria ochroleuca*. Flower and outer tepal ×1; ovary, stamens and style branches ×3.

long, slightly tapering from the base to the apex, smooth; *anthers* 4.5–8 mm long, diverging, straight or slightly arched. *Ovary* 13–16 mm long; *style* dividing just above the anther base; *branches* 5–6.5 mm long, diverging, straight, about as wide as the anthers, the stigma bilobed, held above the anther apex; crests absent, or very short, not exceeding the stigmas and obtuse. *Capsule* 2–3(–4) cm long, cylindrical, with a short beak ca. 1 mm long. *Chromosome number* $2n = 12, 24, 24 + 0\text{–}3B$.

Flowering time: (May–)June–November(–December), usually later at higher altitudes.

Distribution: mountains and flats, from Caledon and Hermanus in the south, to the Olifants River Mountains and Cold Bokkeveld Mountains as far north as Citrusdal; only on sandstone-derived soils; blooming only in the winter-spring after fires; Fig. 12.

Homeria ochroleuca is typically a montane species and it is a common constituent of the mountain fynbos flora in the western half of the Cape Floristic Region, from Hermanus to Citrusdal. It is seldom seen in flower except in seasons immediately following a severe veld fire, and then it appears in large numbers on mountain slopes and flats where the soil is derived from sandstones of the Table Mountain Series. Higher altitude forms sometimes have two or three leaves, although most collections from all altitudes are of solitary-leafed plants. *Homeria lucasii*, reduced to synonymy here, represents the bifoliate form. The original

locality of the type collection of the synonym is unknown. Other two- or three-leafed collections are *Leighton 1332* from the foot of the Witsenberg (the gathering includes single-leafed plants); and *Goldblatt 4205A,* from Fonteintjiesberg near Worcester.

The flower of *H. ochroleuca* is unique in *Homeria* in having diffuse nectaries, located in the median area of the claw of both the inner and outer tepals, whereas all other species have a distinct nectary at the base of only the outer tepals. This character is of little value in identifying dry material as the nectary is always difficult to see. *Homeria ochroleuca* can, however, be distinguished from related single-leafed species by its wide tepal cup, glabrous tepals and filament column, large and diverging anthers and style branches, the latter without obvious crests. Difficulties with identification arise only when flowers are poorly pressed.

Flowers of *H. ochroleuca* last three days, opening in mid morning on the first day, and fading gradually during the third day. The flowers have a strong, rather sickly sweet odor, which attracts flies, the main pollinators. At lower altitudes *H. ochroleuca* often occurs together with or near *H. collina,* and occasional natural hybrids between the two are sometimes found.

There is a slight problem in typifying *H. ochroleuca,* since Salisbury, when giving a specific name to Ker's *Moraea collina* var γ cited the *Botanical Magazine* figure 1283 which is *M. spicata* (i.e., *Homeria elegans*) instead of fig. 1103, the type figure for *M. collina* var. γ. Since *H. ochroleuca* was intended as a new name for *M. collina* (γ) and its (albeit very brief) diagnosis serves as the description also for *H. ochroleuca,* the *Botanical Magazine* figure 1103 is the type, and we must assume Salisbury simply erred in citing figure 1283.

SOUTH AFRICA. CAPE: 32.19 (Wuppertal): Elandskloof (CA), *Barker 3097* (NBG); *Lewis s.n.* (BOL-21857, BOL-31576, PRE). Middelberg, Elandskloof, *Thompson 2938* (MO, STE).

33.18 (Cape Town): Mamre hills (AD), *Barker 1767* (NBG). Near Ganzekraal turnoff from Darling road, *Barker 789* (NBG). Camps Bay Drive (CD), *Steyn 183* (NBG); *Morris 129* (NBG). Slopes above Camps Bay, *Kensit s.n.* (BOL-31575). Platteklip, *Marloth 6276* (PRE). Table Mt., *H. Bolus 2811* (K). Devils Peak, 1200 ft, *H. Bolus 3790* (BOL, K); *MacOwan s.n.* (SAM-20642). Newlands, *Wolley Dod 594* (K); *Page s.n.* (BOL-16188). Wellington (DB), *Moss 2891* (J). Langverwacht, Kuils R. (DC), *Oliver 4773* (K, STE). Hercules Pillar (DD), *Salter 8670* (BOL). Jonkershoek, *Werdemann & Oberdieck 342* (B).

33.19 (Worcester): Gydo (AB), *Leipoldt 3016* (BOL, K). Base of the Witsenberg (AC), *Leighton 1332* (BOL). Michells Pass (AD), *Walgate 372* (BOL, NBG). Near Lakenvlei (BC), *Phillips 2065* (SAM). Bains Kloof (CA), *Barker 4658* (NBG). Fonteintjiesberg, 4000 ft (CB), *Goldblatt 4205A* (cult.) (MO). French Hoek Pass (CC), *Bond 362* (NBG); *Barker 243* (NBG); *Boucher 2302* (K, PRE, STE).

34.18 (Simonstown): Kalk Bay Mt. (AB), *Barker 4202* (NBG); *Goldblatt 2142* (MO, NBG, WAG), *3651* (MO, PRE). Clovelly, *Walgate s.n.* (BOL-31553, SAM-54332). Chapmans Peak, *Van Niekerk 463* (NBG). Karbonkelberg, *Compton 13631* (NBG), *16360* (NBG); *Leighton 682* (BOL). Imhoffs Gift, *Barker 4574* (NGB). Hillside above Kommetje, *Lewis 2497* (SAM). Simonstown, *Zeyher 113* (BOL). Slopes of Constantiaberg, *Acocks 4407* (S). Above Smithswinkel Bay (AD), *Phillips s.n.* (G, M); *Barker s.n.* (BOL-20959, K). Cape Point, *Rogers 28565* (GRA, J, K, Z), *30147* (G, Z). Disa Gorge, Bettys Bay (BD), *Boucher 1396* (K, PRE, STE, WAG).

34.19 (Caledon): Flats between French Hoek and Viljoens Passes (AA), *Davis s.n.* (SAM-60202). Lebanon Forest Reserve, *Kruger 481* (NBG, STE). 2 km E of Caledon, on Swartberg slopes (AB), *Goldblatt 4127* (MO, PRE, WAG). Caledon, *Penther 760* (Z).

Without locality: *Lucas s.n.* (cult. Rondebosch) (BOL-18572); *H. H. Bolus s.n.* (ex hort. Lucas, cult. Kenilworth) (BOL-18752, -18640).

10. Homeria bulbillifera Lewis, J. S. African Bot. 11: 117. 1945. TYPE: South Africa, Cape, Caledon Div., Riviera, *Purcell s.n.* (SAM-54696, holotype).—FIG. 13.

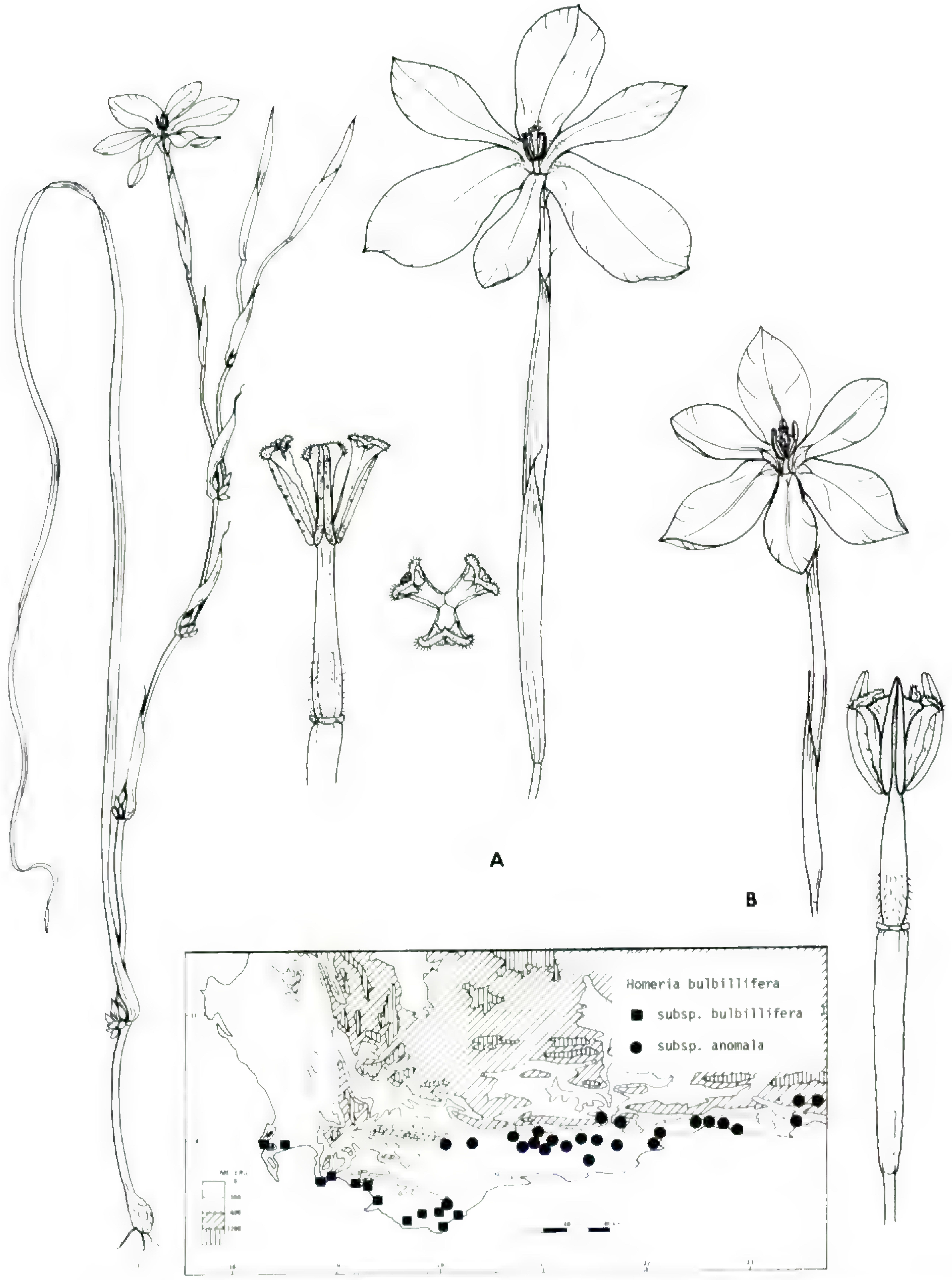

FIGURE 13. Morphology and distribution of *Homeria bulbillifera*.—A. Subsp. *bulbillifera*.—B. Subsp. *anomala*. Habit ×0.4; flowers ×1; ovary, stamens and style branches ×3.

Plants 30–50(–60) cm tall. *Corm* 10–20 mm in diameter, sometimes bearing many cormlets round the base. *Leaf* solitary, usually inserted at or near ground level, rarely far above ground level, longer than the stem, channeled, 5–10 mm wide. *Stem* erect or more or less trailing, usually much branched, flexed above

the leaf sheath and above the stem bracts, the latter 3.5–8 cm long, the stem sometimes bearing several to many cormlets in the axils of the leaf and stem bracts. *Spathes* 4–8 cm long, the outer about half the inner, the inner elongating after flowering, sheathing the young fruits. *Flower* pale or deep yellow, occasionally pale pink, or flushed pink-orange, the nectar guide dark yellow spotted green, the tepals forming a small narrow cup 7–10 mm deep, enclosing the filaments and the lower part of the anthers, spreading above; *outer tepals* 23–38 mm long, the claw 9–11 mm long, the limb 10–16 mm wide, obovate; inner tepals slightly smaller, 7–12 mm wide. *Filaments* united, 6–8 mm long, the column cylindrical, papillate or smooth; *anthers* 4–6 mm long, diverging. *Ovary* 7–12(–13) mm long; *style* dividing at the apex of the filament column; *branches* diverging (2.5–)3–6 mm long, usually just shorter than the anthers, the stigma upright, pressed against the anther in the middle, receptive on the inner lateral surface; crests 1–2 mm long, extending inwards. *Capsule* 17–20(–22) mm long, cylindrical-clavate. *Chromosome number* $2n = 12, 18, 24$.

Flowering time: August–early October inland, September–early November along the coast.

Distribution: southern Cape, from the Peninsula in the west to the Albany district in the east, south of the Langeberg-Outeniqua axis, and most frequent between Elim and Knysna, along the coast, and in the Langeberg foothills; Fig. 13.

Homeria bulbillifera is a common species in the southern Cape, but surprisingly was only described in 1945 (Lewis, 1945). Previously the species had been included either in *H. collina*, or *H. ochroleuca*, or simply left unnamed.

The coastal forms, which are strongly cormiferous, are unmistakable since the only other species of *Homeria* with this characteristic is a Natal form of *H. pallida*. However, even nonbulbilliferous forms are fairly easy to distinguish from other single-leafed species by their open flowers, with the narrow tepal cup enclosing only the filaments, while the anther and well-developed style branches and crests extend well above the cup. The single leaf is usually inserted at or very close to the ground, but plants from the drier valleys on the northern edge of its range are often confusing as the leaf may be inserted rather high above ground.

Two subspecies are recognized. The typical subsp. *bulbillifera* is coastal and always found on sand or limestone. It is usually robust and has a well-developed cormiferous habit. Subspecies *anomala* occurs inland from the coast, mainly in renosterbos veld, on the rolling clay plains of the southern Cape, and it extends into the sandy and rocky valleys of the Riviersondered and Langeberg mountains. It may be as robust as subsp. *bulbillifera* but in drier habitats is a much smaller plant, with the dwarfing extending to the flowers as well.

Homeria bulbillifera, with its more or less basal leaf, several to many branches, and open flower with distinct style branches and crests is one of the least specialized species of section *Homeria*. It is probably close to the ancestral forms which gave rise to the several specialized species of the section which occur to the west and northwest of its range.

KEY TO THE SUBSPECIES

1. Stems conspicuously cormiferous at the aerial nodes, the cormlets breaking through the bracts .... a. subsp. *bulbillifera*
1'. Stems not cormiferous at the nodes (rarely a single corm may develop at some nodes, always concealed by the bracts) .... b. subsp. *anomala*

a. Subspecies **anomala** Goldbl., subsp. nov. TYPE: South Africa, Cape, Witsands road near Ossekop, *Goldblatt 4885* (MO, holotype; BR, K, NBG, PRE, WAG, isotypes).—FIG. 13B.

Folium basale vel in inferiore parte caulis insertum. Caulis non cormiferus in nodis, usitate pluriramosus. Spathae 4–7 cm longae, graciles. Flores usitate breviores quam subsp. *bulbillifera*; tepala exteriora 26–35 mm longa, 10–15 mm lata; interiora 23–32 mm longa. Filamenta 6–8 mm longa; antherae 5–6 mm longae, ramos styli excedentes.

Leaf basal or inserted in the lower part of the stem, usually erect, or trailing distally. *Stem* not cormiferous at the nodes, the branches usually many, (1–)10–20, the stem bracts 3–6 cm long. *Spathes* 4–7 cm long, slender. *Flowers* usually smaller than subsp. *bulbillifera*; *outer tepals* 26–35 mm long, 10–15 mm at the widest; inner tepals 23–32 mm long. *Filaments* 6–8 mm long; *anthers* 5–6 mm long, longer than the style branches, the apices curving inward after anthesis. *Chromosome number* $2n = 12, 24$.

Flowering time: August–October.

Distribution: Stormsvlei and Bredasdorp in the west, along the Langeberg-Outeniqua axis and as far east as the Albany district; on clay or sand, and inland or coastal; Fig. 13.

Subspecies *anomala* is more variable than subsp. *bulbillifera* and occurs in a wide range of habitats from moist sandy stream banks to the dry interior valleys of the Langeberg and Riviersonderend mountains. Flower size and point of leaf insertion are characteristics in which the two subspecies differ. Flowers of subsp. *anomala* are usually smaller, and the outer tepals rarely reach 35 mm in length. The produced leaf may be basal as in subsp. *bulbillifera*, but it is often inserted shortly, to well above ground level. Plants will on occasion have one or two cormlets at some nodes, but this development is much less noticeable than the proliferation characteristic of subsp. *bulbillifera* (e.g., *Loubser 885*, Swellendam) where the many cormlets break through the stem bracts. These forms do, however, represent intermediates between the subspecies and determination becomes rather arbitrary.

SOUTH AFRICA. CAPE: 33.20 (Montagu): Hill below Crown Mt., Swellendam (CD) *Wurts 305* (NBG); *Marsh 845* (STE).

33.21 (Ladismith): Cloetes Pass-Wagenbooms, N of Langeberge (DC), *Goldblatt 4168* (MO). Cloetes Pass (DD), *Goldblatt 4157* (K, MO, PRE, S, WAG).

33.22 (Oudtshoorn): Edge of Rondevlei, near Sedgefield (DC), *Bayliss 6828* (M). Klein Swart R. valley, *Gillett 1244* (BOL, STE).

33.23 (Willowmore): 22 km W of Lauterwater (CB), *Marsh 1409* (K, STE). Lauterwater, W of river (DC), *Fourcade s.n.* (STE).

33.26 (Grahamstown): Cradock road, Albany distr. (A), *Bayliss 6858* (MO).

34.19 (Caledon): The Poort, Bredasdorp (DB), *Wasserfall 381* (NBG), *400* (NBG); *Goldblatt 4856* (C, LE, MO, PRE, WAG).

34.20 (Bredasdorp): Stormsvlei Kloof (AA), *Goldblatt 4130* (MO, PRE, WAG). 25 km W of Swellendam, Bromberg slopes, *Goldblatt 4883* (MO, S). Swellendam (AB), *Loubser 885* (NBG), *2089*

(NBG). Bontebok Park, *Grobler 420* (STE); *Barnard 605* (PRE); *Liebenberg 6354* (PRE, STE). Witsands road near Ossekop (BA), *Goldblatt 4885* (BR, K, MO, NBG, PRE, WAG). Near Buffeljagsrivier, *Goldblatt 4137* (MO). Heidelberg-Swellendam (BB), *Rycroft 2849* (NBG). Near Heidelberg, *Galpin 4653* (BOL, GRA, K, PRE).

34.21 (Riversdale): Riversdale (AB), *Anderson s.n.* (BOL-15456). Hills near Riversdale, *Muir 2695* (BOL). 17 mi W of Albertinia, *Lewis 5568* (NBG). Riversdale-Stilbaai, limestone hills (AC), *Goldblatt 4151* (MO, PRE). Albertinia (BA), *Fries et al. 1366* (K, LD, PRE, S); *Muir 1089* (BOL). 10.1 mi E of Albertinia, *Thompson 550* (K, PRE, STE). Herbertsdale turnoff from Mossel Bay road, (BB), *Schlieben & Ellis 12344* (PRE, STE). Near Melkhoutfontein (BD), *Thompson 2014* (PRE).

34.22 (Mossel Bay): Meadows near Mossel Bay (AA), *Cassidy 240* (NBG). Between Groot and Klein Brak rivers, *Mauve 4571* (K, PRE, STE). W side of Great Brak R., *Burchell 6149* (K). Groenvlei-Wilderness (BB), *Martin s.n.* (NBG-59325). Sedgefield, edge of Swartvlei, *Goldblatt 4920* (MO). Belvedere, *Gillett 2191* (STE).

34.23 (Knysna): Knysna Heads (AA), *Gillett 2177* (STE). Near Knysna, *Wurts 2265* (NBG). Matjesfontein, Keurbooms R. (BB), *Fourcade 4803* (K).

34.24 (Humansdorp): Humansdorp-Jeffreys Bay (BB), *Fourcade 4005* (K).

Without precise locality: Knysna-George, *Rodin 1318* (BOL, K, PRE).

b. Subspecies **bulbillifera**.—FIG. 13A.

Leaf basal, often trailing. *Stem* bulbilliferous at the nodes, the branches 1–5(–10), usually from the upper nodes, the stem bracts 3.5–6 cm long. *Spathes* 5–8 cm long, thick and inflated. *Flowers* fairly large; *outer tepals* 23–38 mm long, (10–)14–16 mm at the widest; inner tepals 22–32 mm long. *Filaments* 6–7 mm long; *anthers* 4.5–6 mm long, usually about as long as the style branches, sometimes longer. *Chromosome number* $2n = 12$ (18).

Flowering time: mid September–November.

Distribution: Cape Agulhas to Peninsula; sandy soils, near the coast; Fig. 13.

Subspecies *bulbillifera* is always easily recognized by its conspicuous cormiferous habit. Although usually bearing several branches, the stems often appear attenuated. The lower nodes often lack branches, and the stem sometimes becomes more or less trailing. This subspecies is restricted in distribution to sandy or rarely limestone-derived soils and occurs mainly along the coast. Many collections of this subspecies have no developing capsules, and it seems likely that at least some populations are sexually sterile. The copious cormlets presumably ensure propagation of these sterile forms.

SOUTH AFRICA. CAPE: 34.18 (Simonstown): Karbonkelberg, Cape Peninsula (AB), *Compton 16358* (NBG); *Leighton 419* (BOL), *681* (BOL, PRE, SAM); *Goldblatt 2988* (BR, C, MO, S, WAG). Little Lions Head, *Compton 18576* (NBG). Rondevlei, Cape Peninsula (BA), *L. Bolus s.n.* (BOL-22944, K). Bettys Bay (BD), *Loubser 960* (NBG). Cape Hangklip, *Goldblatt 2988* (K, MO, S, WAG).

34.19 (Caledon): Onrus R., near sea (AC) *Gillett 4399* (MO). Hawston, *Marloth 9197* (PRE). Hermanus, Campsite (AD), *Lussem 9* (NBG). Gansbaai (CB), *Gillett 4322* (BOL, K, MO). Ratel River flats near Quoin Pt. (DA), *Goldblatt 470* (BOL). The Poort, Bredasdorp (DB), *Lewis s.n.* (BOL-21231). 22 m from Arniston towards Elim, *Marsh 916* (PRE, STE).

34.20 (Bredasdorp): Die Mond (CA), *Compton 22118* (NBG). Near Struys Bay (CC), *Leipoldt 3569* (BOL).

11. Homeria comptonii L. Bolus, S. African Gard. 19: 294. 1929. TYPE: South Africa, Cape, near Villiersdorp, *Compton s.n.* (BOL, lectotype; K, isolectotype).—FIG. 14.

H. maculata Klatt, pro parte et sensu auct. (Linnaea 34: 627. 1866); Baker, Fl. Cap. 6: 27. 1896, pro parte.

FIGURE 14. Morphology and distribution of *Homeria comptonii*—both maculate and unmarked flowered forms. Habit ca. ×0.5; flowers, outer tepal and corm ×1; ovary, stamens and style branches ×1.5, the top view much enlarged.

Plants 18–30 cm tall. *Corms* 10–15 mm in diameter. *Leaf* solitary, inserted at or near ground level, linear, canaliculate, erect, or if much exceeding the stem, trailing. *Stem* erect, bearing several branches, the stem bracts 4–6 cm long. *Spathes* 7–10 cm long at flowering time, the inner initially about twice the outer, much elongating after flowering, and enclosing the capsules. *Flowers* large,

yellow entirely, or pink to orange with a yellow center, with or without large dark green nectar guides on the outer or both tepal whorls, the tepals not clearly divided into claw and limb, but the lower parts forming an open cup and the upper parts patent, to slightly recurved, heavily and sweetly scented; *outer tepals* 32–52 mm long, glabrous, often distinctly pandurate or spatulate, 13–18 mm wide, widest in the upper third; inner tepals 30–50 mm long, 8–15 mm wide. *Filaments* united, 6–8 mm long, pubescent in the lower two-thirds, wide at the base, tapering towards the apex; *anthers* (8–)10–13 mm long, diverging, usually shorter than the style branches, occasionally just reaching or exceeding the stigmas. *Ovary* ca. 18 mm long, entirely or partly enclosed in the spathes; *style* dividing 2.5–5 mm above the anther base; *branches* diverging, 6–10 mm long, the stigma lobe spread horizontally, with two erect to incurved crests ca. 1 mm long, the stigma usually well above the apex of the anthers. *Capsules* initially enclosed in the inner spathe, 25–30 mm long, cylindrical. *Chromosome number* $2n = 12$.

Flowering time: late August–September.

Distribution: Caledon district, from Villiersdorp and Bot River west to Caledon and Akkedisberg Kloof; heavy clay soils; Fig. 14.

For many years the yellow-flowered form of *Homeria comptonii* with green markings on the lower part of the tepals was known as *H. maculata* Klatt. One of the specimens cited by Klatt in the description of the species is the maculate form of *H. comptonii* (*Ecklon & Zeyher Irid 38,* "Langehoogde") but the other, *Ecklon & Zeyher Irid 259,* is *Moraea insolens* Goldblatt, and this was made the lectotype of *H. maculata,* which thus became a synonym of *M. insolens* (Goldblatt, 1971b).

The large-flowered, typical form of *H. comptonii* has clear yellow, or orange blooms, and occurs in the northern part of the range of the species, between the Bot River-Caledon main road and Villiersdorp. H. M. L. Bolus who described *H. comptonii* in 1929 believed it distinct from *H. maculata,* although closely related. Further collecting in the Caledon-Bot River area has revealed a wide range of variants between the bright orange, large-flowered plants in the north, and yellow-flowered plants with green spots, east and south of Bot River. Thus populations northeast of Bot River, e.g., *Goldblatt 3997,* have unmarked yellow, or pale orange flowers; plants to the southeast near the Leeu River have yellow flowers with markings on the outer and sometimes the inner tepals, e.g., *Goldblatt 3990*; and populations further east at the foot of Babylons Tower, e.g., *Goldblatt 4020, 4022,* consist of plants with yellow or orange or cream-colored flowers with or without green markings on the tepals. In all characteristics other than flower color and marking, plants from all these populations are essentially alike, being distinguished by the single, basal leaf, comparatively large flower with pandurate to spatulate tepals, a strong sweet scent, style dividing well above the apex of the filament column, and style branches usually exceeding the anthers.

Homeria comptonii is closely related to *H. elegans,* and although the two can usually be distinguished with ease, some populations of *H. comptonii* may be confused. Differences between the two species are discussed in detail under *H. elegans,* the following species in the treatment.

Milne-Redhead (1937) believed *H. comptonii* (though not *H. maculata*) to be

conspecific with *H. collina,* in which he also included *H. ochroleuca* and *H. flaccida* (as *H. aurantiaca*), and he explained his reasons under a good illustration of *H. comptonii* (*Botanical Magazine,* tab. 9457) named *H. collina.* I do not wish to dwell on this point of view, except to point out that no opinion concerning the systematics of *Homeria* is of much value if based mainly on the knowledge of dried plants. In the field the four species Milne-Redhead places in *H. collina* appear morphologically distinct, and each has its own geographic range, characteristic habitat, ecological preference, and flowering time. All occur in parts of the Caledon district, and can always be distinguished, with ease, when alive.

SOUTH AFRICA. CAPE: 34.19 (Caledon): Near Bot River (AA), *Guthrie s.n.* (BOL-16910). Bot R. distr., *Garside 4479* (K), *4496* (K). N of Bot R. near Vyeboom, *Goldblatt 289* (BOL). Near Villiersdorp (AB), *Compton s.n.* (BOL, K). "Langehoogde," *Ecklon & Zeyher Irid 38* (B). N slopes of Eseljagt Pass, *Barker 10577* (K, MO, NBG); *Goldblatt 2633* (MO, NBG). Goedvertrou-Caledon/Villiersdorp road, *Goldblatt 3997* (K, MO, PRE, WAG, US). Main road Bot R.-Boontjieskraal, *Pillans 6675* (BOL, K). Caledon-Bot R., burnt area, *Fairall 187* (BOL, NBG). Caledon-Villiersdorp, *Barker 19* (K), *20* (BOL, K). S of Bot R. between Albertyn and Leeu River (AC), *Barnard s.n.* (MO, NBG-100438, PRE); *Goldblatt 3990* (BR, MO, S). S of Caledon-Bot R. road, towards foot of Babylons Tower (AD), *Goldblatt 4020* (MO, US), *4022* (K, MO, NBG, PRE, WAG). Akkedisberg Pass, 10 km N of Stanford (BC), *Goldblatt 4845* (K, MO, NBG).

12. **Homeria elegans** (Jacq.) Sweet, Hort. Brit., ed. 1: 395. 1827; Baker, Fl. Cap. 6: 27. 1896.—FIG. 15.

Moraea elegans Jacq., Pl. Hort. Schoenbr. 1: 6, *tab. 12.* 1797. TYPE: South Africa, Cape, exact locality unknown, illustration in Pl. Hort. Schoenbr. 1: *tab. 12.*
Sisyrinchium elegans (Jacq.) Willd., Sp. Pl. 3: 577. 1801.
Moraea spicata Ker, Bot. Mag. *tab. 1283.* 1810. TYPE: South Africa, Cape, exact locality unknown, illustration in Bot. Mag. *tab. 1283.*
Homeria spicata (Ker) Sweet, Hort. Brit., ed. 1: 395. 1827.
H. metelerkampiae L. Bolus, S. African Gard. 18: 116. 1928. TYPE: South Africa, Cape, cultivated in Mr. Metelerkamp's garden, Wellington, origin unknown, (but possibly near Genadendal, fide *Marloth 9253,* PRE), *Metelerkamp s.n.* (BOL-31545, lectotype; K, isolectotype).

Plants 15–30 cm tall. *Corms* 10–12 mm in diameter. *Leaf* solitary, inserted at or near ground level, linear, channeled, to 10 mm wide, erect, or if much exceeding the stem, trailing. *Stem* erect, bearing few to several branches, the stem bracts 5–7 cm long. *Spathes* 7–10 cm long, the inner initially about twice the outer, much elongating after flowering and enclosing the capsules. *Flowers* large, yellow in the center, with a large green blotch in the mid or upper third of each outer tepal, and usually orange distally, the tepals not clearly divided into claw and limb but the lower parts more or less forming a cup, and the upper parts patent, strongly and sweetly scented; *outer tepals* 28–35 mm long, oblong or ovate, the claw narrow, 13–15 mm wide, widest in the lower third; inner tepals 26–38 mm long, about as long or occasionally longer than the outer, 10–11 mm wide. *Filaments* united, 5–7 mm long, the column pubescent in the lower two-thirds, widest at the base, tapering towards the apex; *anthers* 8–10 mm long, diverging, usually exceeding the style branches, the tips curving inward after anthesis. *Ovary* 12–15 mm long, usually entirely included in spathes; *style* branching shortly above the anther base; *branches* diverging, ca. 6 mm long, shorter than the anthers; the stigma erect, appressed to the anthers; crests 1–2 mm long, incurved. *Capsule* included in the spathes, to 25 mm long, cylindrical. *Chromosome number* $2n = 12$.

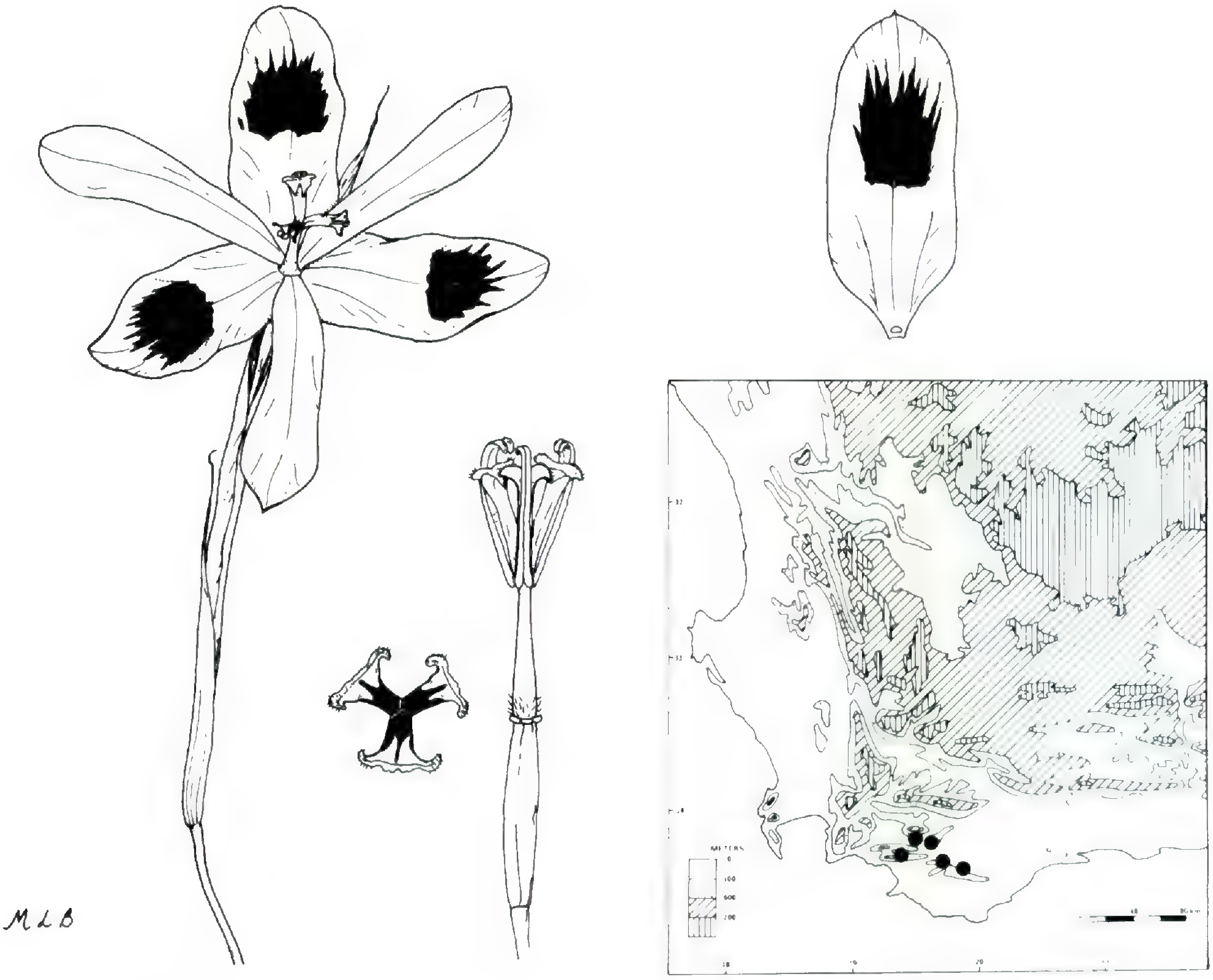

FIGURE 15. Floral morphology and distribution of *Homeria elegans*. Flower and outer tepal ×1; ovary, stamens and style branches ×1.5, the top view much enlarged.

Flowering time: late August–early October.

Distribution: Caledon district, from Caledon eastwards along the foot of the Zwartberg, and north of the Klein River mountains from Tesslaarsdal to Fairfield and southeast to Bredasdorp; clay soils; Fig. 15.

Homeria elegans is closely related to *H. comptonii*, and the two species have complementary ranges in the Caledon and Bredasdorp district in the southwestern Cape. They are generally easy to distinguish, although some populations of *H. comptonii* approach *H. elegans* in appearance. Generally *H. elegans* has oblong outer tepals, sometimes broadest in the lower half, and large green blotches in the mid or upper third of the outer tepals. The style branches divide at the top of the filament column and are distinctly shorter than the anthers. In contrast *H. comptonii* has spatulate or pandurate outer tepals, either unmarked or with markings in the mid or lower third of the tepals. The style branches divide well above the anther base and exceed the anthers by 2 mm or more.

The type of *H. elegans*, an illustration published by Jacquin, shows all the critical features of the plant, except that the outer tepals are not quite oblong. They have a barely perceptible narrowing in the middle, and seem as wide at the apex as at the base. However, the point of division of the style and the long

anthers clearly accord with wild plants assigned to this species. *Homeria elegans* is variable in floral markings. The yellow flowers are most often marked with large oval green blotches on the upper half of the outer tepals which are bright orange distal to the markings. Occasionally the tepals are not tipped with orange, as in the type figure, and sometimes the markings themselves are partly or entirely orange on a yellow background.

With some hesitation I place *H. metelerkampiae* as a synonym of *H. elegans*. This species, known only from plants cultivated in a garden in Wellington, may have come from near Genadendal, if the note to this effect on the label of *Marloth 9253* is correct. It is very like *H. elegans* in most critical features, having a single, basal leaf and similar-sized spathes and flowers. Like *H. elegans,* the style divides near the top of the filament column, and the anthers exceed the style branches. The only feature that is discordant is the markings, which in the yellow-flowered *H. metelerkampiae* are large green blotches located on the reverse of all six tepals. In contrast, all known wild forms of *H. elegans* have markings on the inside of the outer tepals. *Moraea spicata* is probably also a synonym of *H. elegans*. The type of this species is a figure in the *Botanical Magazine,* but is poorly drawn, which may be explained by the fact that the illustration was made from dried material.

Homeria elegans is becoming increasingly rare in the wild as agriculture has spread through the Caledon district, leaving little untouched vegetation in its wake. A few small colonies, along road verges, steeper banks and very rocky sites, remain, but are seriously threatened by road building activities, the spread of agricultural weeds, the effects of fertilizers changing soil fertility, and aerial spraying of weed killers. This *Homeria,* one of the most valuable for horticulture, may well become extinct in the next decade.

SOUTH AFRICA. CAPE: 34.19 (Caledon): Swartberg near Caledon (AB), *MacOwan s.n.* (Herb. Norm. Aust. Afr. 799) (B, G, K, P). Slopes of Caledon Swartberg, *Templeman s.n. sub MacOwan 2613* (S). Caledon-Napier (B), *Barker s.n.* (BOL, K, SAM). Genadendal (BA) (cultivated in Wellington), *Marloth 9253* (PRE). Near Krige, E of Caledon (BB), *Goldblatt 4879* (MO). Kleinrivierskloof (BC), *Zeyher 4073* (GRA, K, P, PRE, S, SAM). Near Tesslaarsdal, *Goldblatt 4095* (K, MO, PRE, S, WAG). 8 mi SE of Oudekraal, *Salter 4799* (BOL, K). Near Fairfield, Caledon-Napier road (BD), *Goldblatt 4852* (MO).

34.20 (Bredasdorp): Bredasdorp district (C), *Van der Byl s.n.* (K).

Without locality: *Sparrman s.n.* (S).

13. **Homeria flaccida** Sweet, Hort. Brit., ed. 1: 395. 1826. TYPE: South Africa, Cape, without locality, illustration in Bot. Mag. *tab. 1612.* 1814 (*H. collina* var. *miniata minor* Ker).—FIG. 16.

Moraea flaccida (Sweet) Steud., Nom. Bot., ed 2, 2: 160. 1840.

Homeria collina (Thunb.) Salisb. var. *flaccida* (Sweet) Klatt, Linnaea 34: 629. 1865.

H. aurantiaca (Zuccagni) Sweet sensu Sweet, Hort. Brit., ed. 2: 498. 1830. (Comb. based on *Sisyrinchium aurantiacum* Zuccagni in Roemer, Coll.: 145. 1809, identity unknown).

Moraea aurantiaca (Zuccagni) A. Dietrich sensu A. Dietrich, Sp. Pl. 2: 485. 1833.

Homeria collina var. *aurantiaca* (Zuccagni) Baker sensu Baker, Handb. Irid. 75. 1892 et Fl. Cap. 6: 28. 1896.

H. breyniana (L.) Lewis var. *aurantiaca* (Zuccagni) Lewis sensu Lewis, Fl. Cape Pen. (ed. Adamson & Salter) 232. 1950.

H. collina var. *bicolor* Baker, Handb. Irid. 75. 1892 et Fl. Cap. 6: 28. 1896. TYPE: South Africa, Cape, Stellenbosch, *Sanderson s.n.* (K, holotype).

H. bicolor (Baker) Klatt in Th. Durand & Schinz, Consp. Fl. Afric 5: 157. 1895.

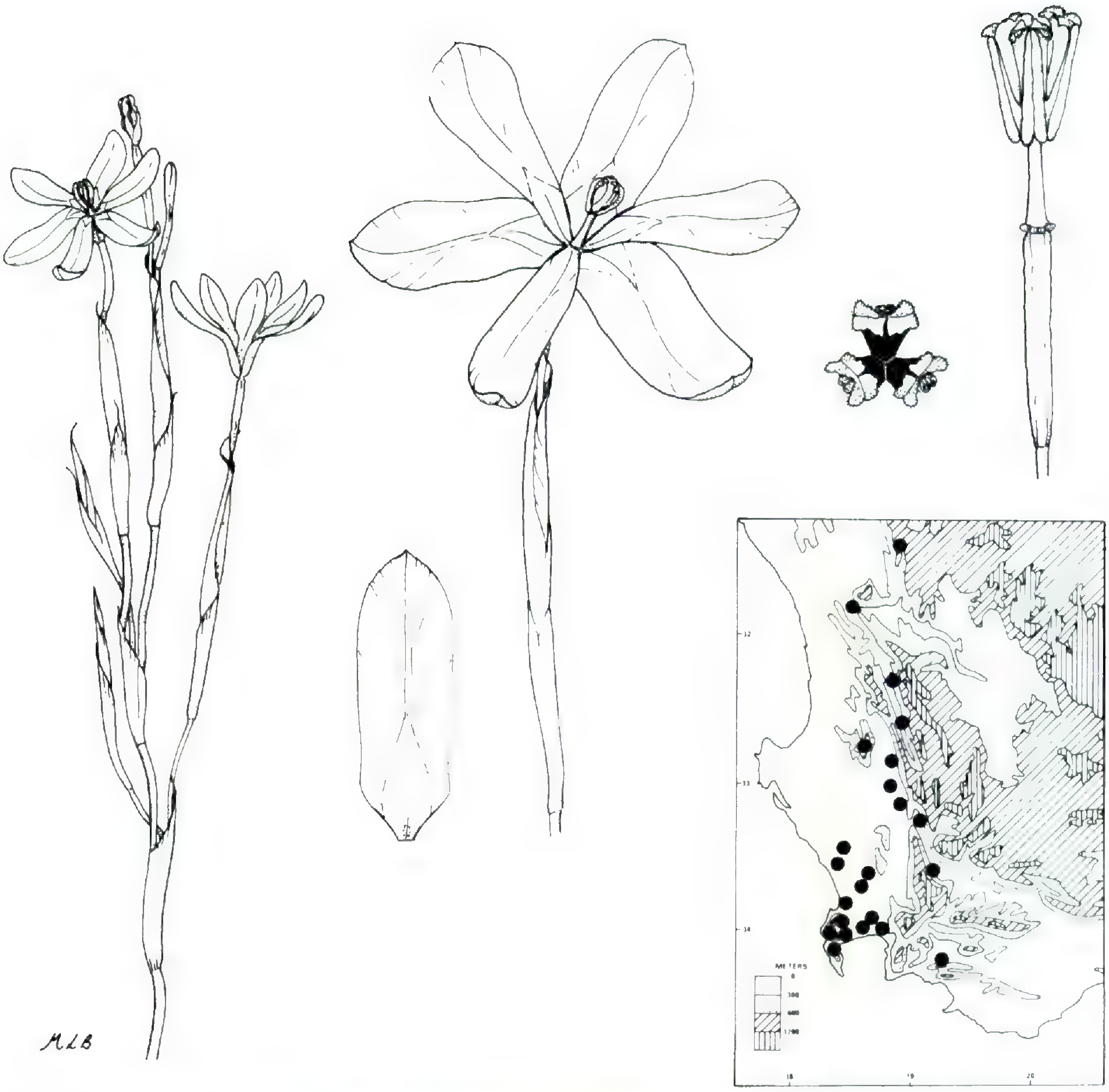

FIGURE 16. Morphology and distribution of *Homeria flaccida*. Flowering branch ca. ×0.4; flower and outer tepal ×1; ovary, stamens and style branches ×1.5, the top view ×2.5.

Plants large, 30–60 cm tall. *Corms* ca. 2 cm in diameter. *Leaf* solitary, inserted above ground level, often well above the ground, canaliculate, exceeding the stem, 9–13 mm wide. *Stem* erect, somewhat flexed above the leaf sheath and above the stem bracts, several branched, the branches flexed outwards above the bracts, the stem bracts 3.5–6 cm long. *Spathes* 5.5–8 cm long, the outer half to two-thirds the inner. *Flowers* salmon orange or yellow, with deep yellow nectar guide and tepal cup, the claw of the tepals forming a 20 mm wide cup, ca. 12 mm deep, including the filaments and part of the anthers; *outer tepals* 35–40 mm long, the claw to 14 mm long, smooth or minutely papillate in the lower part, the limb flaccid, more or less spreading, oblong or slightly wider in the upper third, 13–20 mm wide. *Filaments* united, 7–8 mm long, the column smooth to sparsely papillate-pubescent in the lower half, widest at the base, tapering slightly to the apex; *anthers* 8–11 mm long, contiguous for 3 mm, then slightly diverging. *Ovary* 17–20 mm long; *style* dividing about 3 mm above the anther base; *branches* slightly diverging, to 7 mm long, the stigma bilobed, curved upward above the apex of

the anthers; crests ca. 1 mm long, erect, triangular. *Capsule* 25–55 mm long, cylindrical, tapering near the apex, with a distinct beak ca. 2 mm long. *Chromosome number* $2n = 24, 36$.

Flowering time: late August–October.

Distribution: Caledon district, and from the Peninsula north to Klawer; usually in low lying areas seasonally waterlogged, mainly in sandy soils; Fig. 16.

Homeria flaccida is often confused with *H. collina,* and was until recently (Goldblatt, 1973) regarded only as a variety of that species (Lewis, 1950). *Homeria flaccida* is, in fact, quite distinct and far more widespread and more common than the related *H. collina.* It can be readily distinguished when living by the shape of the flowers, as well as by its robust appearance, many branches, and distinctive habitat and flowering time. In *H. flaccida* the claws of the tepals spread outward and slightly upward, forming a wide, shallow cup and including the filaments. *Homeria collina,* by contrast, is a shorter, few-branched species with suberect tepal claws, which form a narrow cup enclosing the filaments and anthers. When dried, the shape of the flower of *H. flaccida* is lost, but its large size makes identification fairly easy. The tepals, ovary, filaments, anthers, and capsule are amongst the largest in the genus. The outer tepals are usually 35–40 mm long, and the filaments are ca. 8 mm long with the longer anthers up to 11 mm. The ovary, initially 17–20 mm long, elongates after fertilization and may reach a length of 55 mm in the mature capsule, which itself is distinctive in having a pointed beak some 2 mm long. By contrast, tepals of *H. collina* seldom exceed 35 mm, the filaments are 6–7 mm long, and the anthers are slightly shorter being 5–6 mm in length. The ovary in *H. collina* is often as long as that of *H. flaccida* and the capsule may attain a length of over 35 mm. The capsule of *H. collina,* however, has a shorter, rather obtuse beak about 1 mm long.

Homeria flaccida is generally found in low-lying, sandy areas water logged in winter, and it flowers rather late in the season, by which time *H. collina* is usually in fruit. Flowering of the two species may overlap briefly, and natural hybrids have been recorded between the two species (Goldblatt, 1973) on the Cape Peninsula. *Homeria flaccida* is a polyploid species, either hexaploid, $2n = 36$ in the southern part of its range on the Peninsula, in the sandveld to the north and in an outlying population near Klawer, or tetraploid, $2n = 24$, on the eastern Cape Flats and further north along the Berg River south of Porterville. *Homeria collina,* which occurs in a more limited area of the southern Cape Flats and Peninsula and mountain valleys to the east, is consistently tetraploid. The hybrids between the two species were pentaploid, $2n = 30$, and completely sterile.

Homeria flaccida was long considered conspecific with a species originally described as *Sisyrinchium aurantiacum* by Zuccagni in 1809. This idea was first expressed by Sweet who made the combination *H. aurantiaca* (Zucc.) Sweet in 1830, only four years after he had described *H. flaccida,* which he then reduced to synonymy. According to Stafleu (1967), Zuccagni's herbarium in Florence, where presumably the type of *S. aurantiacum* was kept, was so damaged by insects that it was discarded by Parlatore after 1842. The description alone of *S. aurantiacum* is not sufficient for identification of the species, though it seems likely that it belongs to *Homeria.* The leaf is described as radical "folio radicali

canaliculato," while the produced leaf of *H. flaccida* is inserted on the stem well above ground level. In comparing *S. aurantiacum* with *H. collina* Zuccagni mentions it differed from the latter in its "corolla maculata" which adds further to the problem of identifying the species. *Sisyrinchium aurantiacum* seems best rejected on the grounds that it cannot be satisfactorily identified.

SOUTH AFRICA. CAPE: 31.18 (Van Rhynsdorp): 4 km N of Klawer (DA), *Goldblatt 3932* (K, MO, NBG, PRE, S, WAG).

31.19 (Calvinia): Glenridge, Nieuwoudtville (AC), *Thompson 2901* (STE).

32.18 (Clanwilliam): Modderfontein, Clanwilliam (BB), *Gillett 3678* (BOL, STE). Antonies R., Piketberg (DA), *Barker 2600* (NBG).

32.19 (Wuppertal): Near Citrusdal (CA), *Salter 3866* (BOL); *Story 2986* (PRE).

33.18 (Cape Town): Mamre hills (AD), *Barker 1764* (NBG). Mud River, near Ganzekraal, *Goldblatt 308* (BOL). Platteklip, Darling, *Liebenberg 8264* (PRE). Porterville flats (BB), *Loubser 973* (NBG); Twenty Four Rivers-Gouda, *Goldblatt 3924* (BR, MO, PRE). Near Mamre (CB), *L. Bolus s.n.* (BOL-31559). Near Cape Town (CD), *MacOwan s.n.* (Herb. Norm. Austr. Afr. 252) (BOL, K). Liesbeek R., *Zeyher 5014* (SAM). Camp Ground, *Zeyher 4145* (SAM). Rondebosch Common, *Goldblatt 597* (BOL, MO). Milnerton, *Cassidy 253* (NBG). Milnerton dunes, *Compton 16313* (NBG). Kalabaskraal (DA), *Werdemann & Oberdieck 301* (B, K, PRE). Klipheuwel-Durbanville (DC), *Goldblatt 4123* (MO, WAG). Durbanville, *Barker 2061* (NBG). Stellenbosch-Faure (DD), *Goldblatt 4099* (MO). Lynedoch Station, *Goldblatt 4416* (MO, PRE, WAG). Stellenbosch flats, *Garside 67, 1514* (K).

33.19 (Worcester): Tulbagh, roadside (AC), *Hutchinson 362* (GRA, K, PRE). Slanghoek valley (CA), *Barker 9469* (NBG). Bothas Halt, *van Breda 619* (PRE).

34.18 (Simonstown): Theefontein (AB), *Barker 3882* (NBG). Above Smitswinkel Bay, *Barker s.n.* (BOL-31556). Valley Road, Hout Bay, *Goldblatt 4974* (MO). Diep River, *Marloth 7232* (PRE). Bergvliet Farm, werf, *Purcell s.n.* (MO, SAM-93355,6). Somerset Strand (BB), *Page s.n.* (BOL-16230, -16231). Cultivated land, Somerset West, *Theron s.n.* (K).

14. Homeria autumnalis Goldbl., sp. nov. TYPE: South Africa, Cape, Elands Kloof, 23 km E of Citrusdal, *Goldblatt 5504* (MO, holotype; BR, C, K, NBG, NSW, P, PRE, S, STE, US, WAG, isotypes).—FIG. 17.

Planta 16–30 cm alta. Cormus ca. 20 mm in diametro, tunicis fibris nigris, crassis. Folium unicum, basale, apicis crassis. Caulis simplex vel aliquot ramosus. Spathae 4.5–7 cm longae, interior longitudine circa duplo longior exteriore. Flores flavi, ungues tepalorum tubiformes; tepala exteriora 32–40 mm longa. Filamenta connata, 7–9 mm longa, glabra, inclusa; antherae 5–7 mm longae, divergentes. Ovarium 8–9 mm longum, rami styli ca. 3 mm longi, antheras breviores, cristae 2 mm longae.

Plants 16–30 cm high. *Corms* ca. 20 mm in diameter, the tunics of thick black fibers. *Leaf* solitary, basal, ensiform-linear, flat to somewhat canaliculate, sheathing the base of the stem, barely exceeding to slightly shorter than the stem, with a prominent thickened, flat apical part. *Stem* erect, often flexed below the nodes, simple or 2–several branched, the stem bracts 3.5–6 cm long. *Spathes* herbaceous or becoming dry above, 4.5–7 cm long, the inner about twice as long as the outer, the apices tapering, light brown. *Flowers* bright yellow, the nectar guide a slightly darker area above the knee of the outer tepals, the tepal claws erect, forming a narrow tube around the filament column and curving outwards gradually at the anther base, partly enclosing the anthers; *outer tepals* 32–40 mm long, the claw poorly differentiated, ca. 10 mm long, the limb horizontal, to 15 mm at the widest point; inner tepals 30–35 mm long, 8–12 mm at the widest point. *Filaments* united, the column 7–9 mm long, cylindric, smooth; *anthers* diverging, 5–7 mm long, exceeding the stigma lobes and curving inward above. *Ovary* 8–9 mm long, exserted from the spathes; *style* dividing ca. 2 mm above the anther base, ca. 3

FIGURE 17. Morphology and distribution of *Homeria autumnalis*. Habit and corm ×0.5; flower ×1; ovary, stamens and style branches ×2.

mm long; crests 2 mm long, triangular. *Capsule* well exserted, oblong, 8–15 mm long. *Chromosome number* $2n = 12$.

Flowering time: April–early June.

Distribution: known only from Elands Kloof, east of Citrusdal; sandy soil; apparently flowering well only in the years immediately following a fire; Fig. 17.

Homeria autumnalis is unusual in the genus in its early flowering time, April to June, i.e., autumn and early winter. In this it is similar to *H. galpinii*, a species occurring to the south, which typically blooms from May to July, although it is recorded as flowering as early as March and as late as November. Morphologically these two species are also very alike, having similar yellow flowers, thick black corm tunic fibers, and rather short leaves with prominent thickened apices. They differ in one important feature: *H. autumnalis* has a basally inserted, fairly broad, flat leaf, while in *H. galpinii* the leaf is inserted well above the ground and is narrow and channeled. Close examination of the floral structure reveals further differences. The tepals of *H. galpinii* are slightly shorter, generally the outer tepals are 28–33 mm long compared to 32–40 mm in *H. autumnalis*. The filament column of *H. galpinii* is short, 4–5 mm long and conspicuously papillate-pubescent, and both the anthers and filament column are included in the tepal tube whereas in *H. autumnalis* the filament column is 7–9 mm long and smooth, and the anthers are partly exserted from the tube. Similarities between the two species, however, clearly indicate that they are closely related.

The species has apparently been collected only twice, first by C. L. Leipoldt in 1932 and in 1980 by myself. Both collections are from essentially the same locality in Elands Kloof, east of Citrusdal.

SOUTH AFRICA. CAPE: 32.19 (Wuppertal): 22–23 km E of Citrusdal, in Elandskloof (CA), *Goldblatt 5504* (BR, C, K, MO, NBG, NSW, P, PRE, S, STE, US, WAG). Elands Kloof, 13–15 mi from Citrusdal, *Leipoldt s.n.* (BOL-20475).

15. Homeria galpinii L. Bolus, Fl. Pl. South Africa *tab. 417*. 1931. TYPE: South Africa, Cape, Klein Drakenstein Mts., above Salem, *Galpin 10600* (BOL-19420, holotype; K, isotype).—FIG. 18.

Plants medium, 15–30 cm tall. *Corms* 15–25 mm in diameter. *Leaf* solitary, inserted well above ground, channeled, to 10 mm wide, unusually short, 10–20 cm long, not or only shortly exceeding the stem, usually rigid with a prominent pungent apical portion. *Stem* erect, usually flexed above the leaf insertion, simple or few branched, the branches flexed, the stem bracts 4–5 cm. *Spathes* 4–5(–6) cm long, the outer about half the inner. *Flowers* pale yellow, the tepals forming a narrow cup below, 3–4 mm wide, enclosing the stamens and style and spread horizontally above; *outer tepals* 28–33 mm long, the claw 9–10 mm, erect, the limb ovate-oblong, 9–12 mm wide; inner tepals obovate, slightly smaller. *Filaments* united, the column 4–5 mm long, puberulous, broadest at the base, tapering upward; *anthers* 5–6(–8) mm long, diverging slightly from the base. *Ovary* 6–10 mm long; *style* dividing ca. 1 mm above the anther base; *branches* about as long as the anthers or slightly shorter, the stigma arching over the anther apex; crests erect-incurved, to 1 mm long. *Capsule* 12–15(–20) mm long, ellipsoid. *Chromosome number* $2n = 12, 24$.

Flowering time: late March–early August (also November).

Distribution: southern Cape near Elim, through the Hottentots Holland Moun-

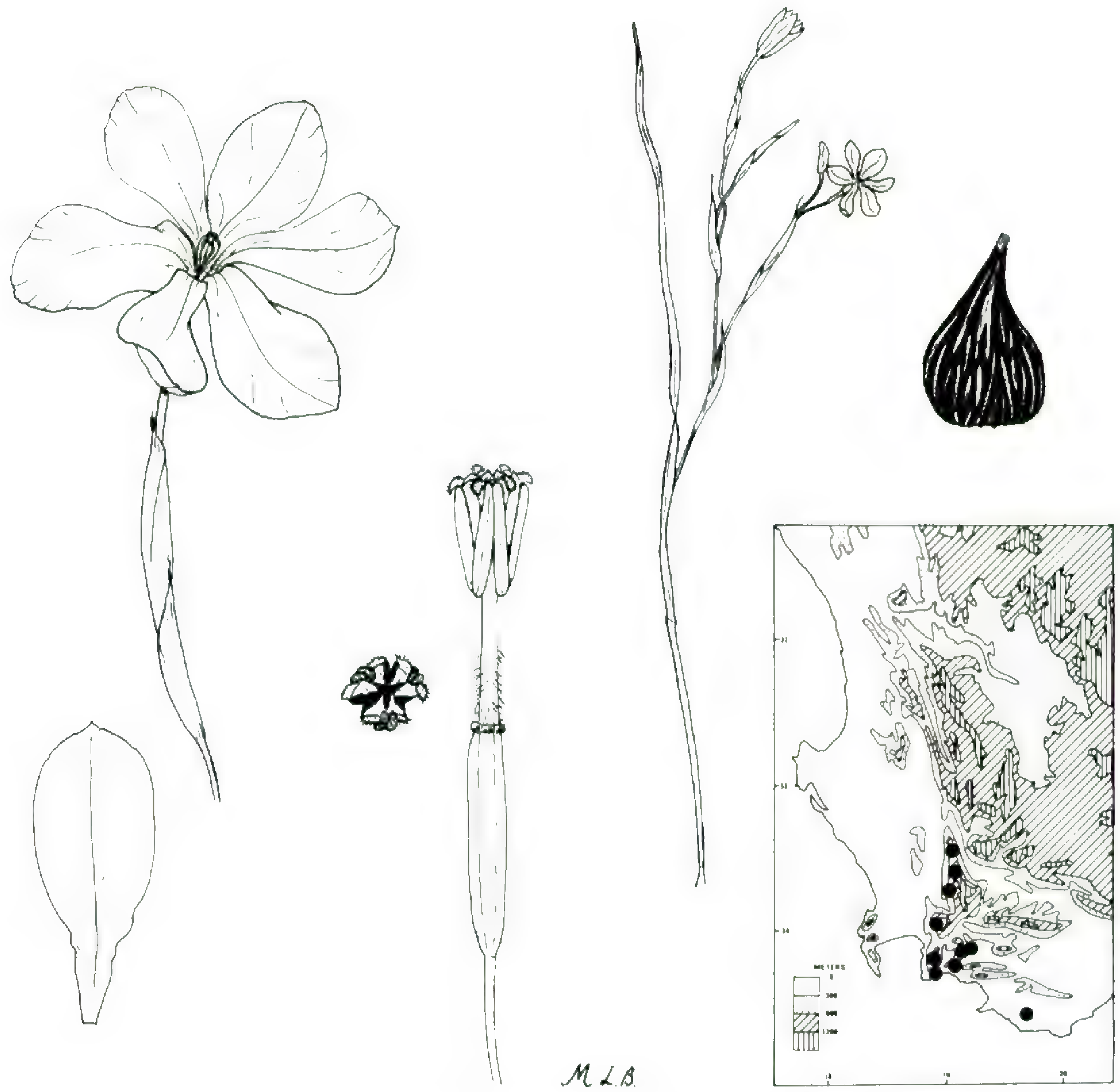

FIGURE 18. Morphology and distribution of *Homeria galpinii*. Habit ×0.3; corm, flower and outer tepal ×1; ovary, stamens and style branches ×1.5.

tains to Bains Kloof, with outlying populations on the Piketberg; on sandy soils; blooming only after fires; Fig. 18.

Homeria galpinii is a distinctive species, unusual in its normally very early flowering, from March to June, though it has once been collected in bloom in November. It grows on the poor sandy soils characteristic of the Cape mountains and blooms only in the season following a fire. *Homeria galpinii* is probably closely related to the morphologically similar *H. autumnalis*, also an early blooming species, but the two can easily be distinguished by their leaf insertion, *H. galpinii* having its leaf set well above the ground and *H. autumnalis* having a basal leaf. It also appears to be related to the southwestern Cape *H. collina*, but confusion with this species is unlikely as *H. collina* has a long trailing leaf in contrast to the very short, apically thickened leaf of *H. galpinii* which seldom exceeds the branches.

The species has a strongly southwestern distribution, and extends east only

as far as Pearly Beach, and north to Bains Kloof, with outlying populations in the Piketberg area, *Pillans 7435, 7485,* representing an unusual longer-leafed form which nevertheless appears to belong to *H. galpinii.* Both tetraploid and diploid populations have been discovered. Tetraploids grow in the Houw Hoek-Kleinmond area and diploids at Hermanus.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): Top of Piketberg Mt. (CC), *Pillans 7485* (K). Hills NW of Moutons Vlei, *Pillans 7435* (BOL).

33.18 (Cape Town): S slopes of Jonkershoek Twins (DD), *Wasserfall 19* (NBG).

33.19 (Worcester): Near Paradise, Bains Kloof (CA), *Heatley s.n. sub Moss 5991* (J). Bains Kloof, *Galpin 12662* (PRE). Klein Drakenstein Mts. (CC), *Galpin 10600* (BOL, K, PRE), *11066* (K, PRE). Mia's Poort, du Toits Kloof Mts., *Esterhuysen 34329* (K, MO, PRE, S, WAG).

34.18 (Simonstown): Kogelberg State Forest (BB), *Durand 180, 193* (STE); Bettys Bay, after fire (BD), *Rycroft 2266* (NBG, STE); *Vogts 35* (K, PRE); *Boucher 694* (PRE, STE). Bettys Bay-Palmiet R., *Loubser 2156* (BOL).

34.19 (Caledon): Houw Hoek (AA), *Schlechter 7785* (E, G, GRA, K, MO, P, PRE, S, US, Z); *Guthrie 2315* (NBG). foot of Houw Hoek Pass, *Goldblatt 1751* (MO, PRE, WAG), *3682* (MO, NBG, PRE, S, WAG). 2 km NE of Kleinmond (AC), *Goldblatt 3688* (MO). Fernkloof, Hermanus, *Goldblatt 5176* (MO). Pearly Beach (DA), *Oliver 4875A* (MO, STE).

16. Homeria collina (Thunb.) Salisb., Trans. Hort. Soc. London 1: 307. 1812. Baker, Fl. Cap. 6: 28, 1896.—FIG. 19.

Moraea collina Thunb., Diss. Moraea 11. 1787. TYPE: South Africa, Cape, hills around Cape Town, *Thunberg s.n.* (Herb. Thunb. 1209, UPS, lectotype).

Sisyrinchium collinum (Thunb.) Cav., Diss. 6: 346. 1788.

Homeria breyniana (L.) Lewis sensu Lewis, J. S. African Bot. 7: 59. 1941. (Based upon *Tulipa breyniana* L., the type of which, an illustration, is not in my opinion identifiable to species (Goldblatt, 1973).)

Plants medium, 18–35 cm tall. *Corms* 12–18 mm in diameter. *Leaf* solitary, inserted well above ground, canaliculate, 4–10 mm wide, exceeding the stem, usually trailing above. *Stem* erect, flexed above the leaf insertion, simple, or few branched, the stem and branches flexed above the bracts, the stem bracts 2–4 cm long. *Spathes* 5–8 cm long, the outer about half the inner. *Flowers* pale yellow or salmon pink, with or without a deep yellow nectar guide edged in green, the tepals forming a cup below, ca. 12 mm deep, enclosing the filaments and anthers, ca. 10 mm wide; *outer tepals* (25–)30–35 mm long, the claw 12–15 mm long, often papillate near the base, the limb spreading horizontally, 10–12 mm wide, obovate; inner tepals to 30 mm long, ca. 10 mm wide. *Filaments* united, the column cylindrical, 6–7 mm long, lightly pubescent in the lower half; *anthers* 5–6 mm long, contiguous in the lower half, slightly diverging above. *Ovary* (10–)14–19 mm long; *style* branching shortly above the base of the anthers; *branches* (5–)6 mm long, diverging slightly and reaching the anther apex, the stigma arched over the anther tips; crests short, ca. 1 mm long, erect-incurved. *Capsule* cylindrical (21–)30–40 mm long with a short obtuse beak ca. 1 mm long. *Chromosome number* $2n = 24$.

Flowering time: late June–early September.

Distribution: restricted in range, extending from the Cape Peninsula east to Bot River, and north to Wellington and Bains Kloof; usually in sandy soil; Fig. 19.

Homeria collina is a common, winter- and early-spring-flowering species on

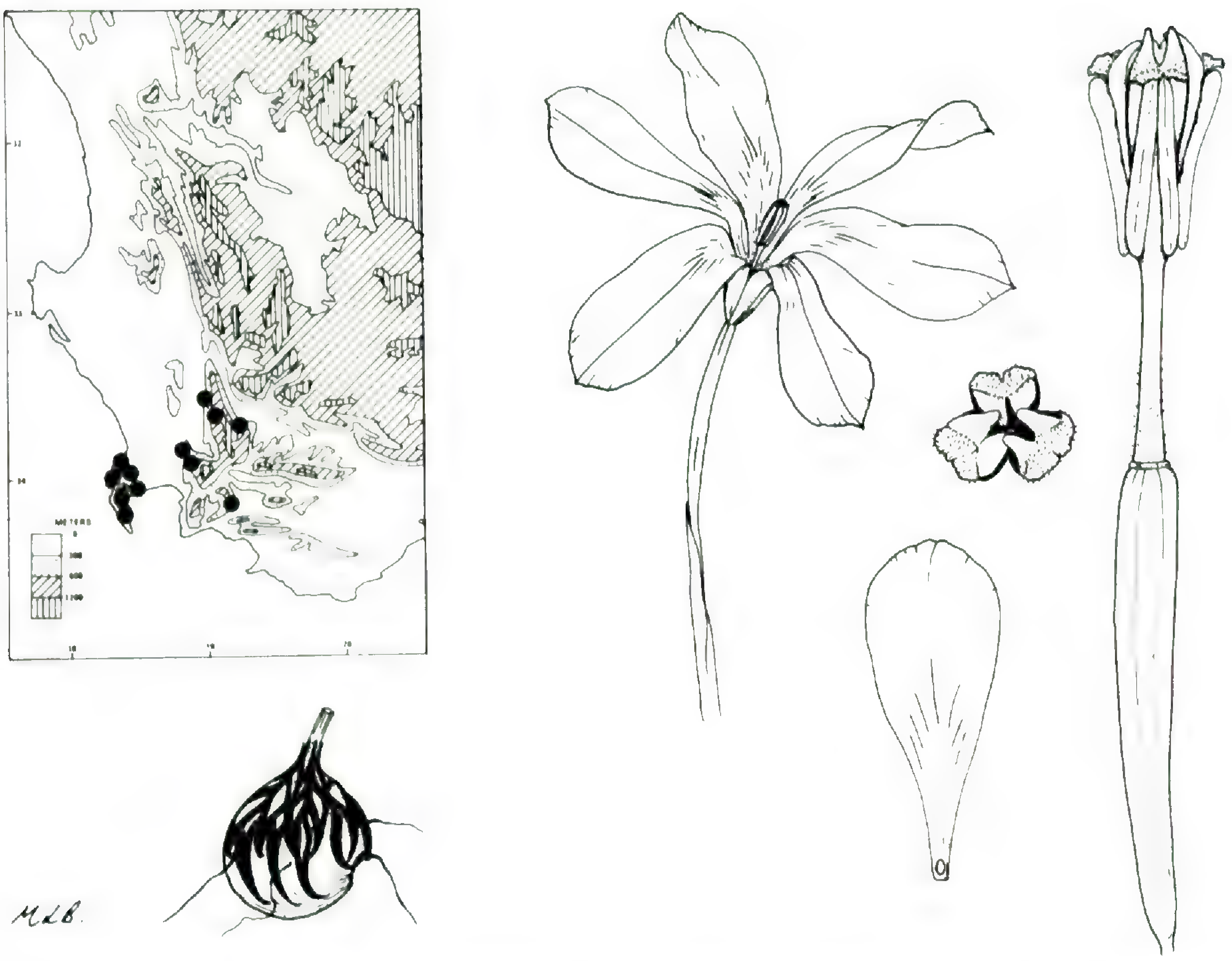

FIGURE 19. Morphology and distribution of *Homeria collina*. Corm, flower and outer tepal ×1; ovary, stamens and style branches ×3.

the Cape Peninsula. Its distribution north and east is rather limited, and it occurs on slopes and in valleys of the Hottentots Holland-Groot Drakenstein-Du Toits Mountains axis. All populations so far examined are tetraploid.

When pressed, it is often difficult to distinguish from several closely related species, including *H. flaccida*, *H. minor* and *H. ochroleuca*, as details of the tepal cup and orientation of the style arms are usually lost. Quantitative characters are fairly reliable and must then be used. *Homeria collina* itself, has a rather narrow tepal cup, which includes the whole stamen and style apparatus, and typically a long ovary and very long capsule, up to 4 cm long. It can be distinguished from the related *H. minor* by floral characteristics; the latter has anthers 3–5 mm long, style branches which divide 2–3 mm above the anther base, an ovary ca. 10 mm long, and a capsule 18–28 mm long. Features of *H. collina* are all slightly larger, though some overlapping occurs. It is equally difficult to distinguish *H. flaccida* when dry, since the shallow, open cup of this species is obscured by pressing. *Homeria flaccida* is somewhat larger in critical floral characters than *H. collina*; thus it has a filament column 7–8 mm long, anthers 8–11 mm long, an ovary 17–20 mm long, and a capsule usually 30–40 mm long. It is also usually taller and more robust than *H. collina*, often has darker pink flowers (though there are also yellow forms), and the capsules have a very characteristic, relatively long acute beak. When these features are present in dried material misidentification should be avoided.

Natural hybrids between *H. collina* and *H. flaccida* have been recorded (Goldblatt, 1973) from the Cape Peninsula. Because *H. flaccida* is hexaploid in this area and *H. collina* tetraploid, the resulting pentaploid, $2n = 30$ hybrid is sterile.

The name *Homeria breyniana* was applied to this species by Lewis (1941) who believed that Linnaeus's *Tulipa breyniana* was an earlier name. I have restored the use of *H. collina* for the species (Goldblatt, 1973) as I am sure the type of *T. breyniana*, an illustration, is not identifiable to species although it is clearly a *Homeria*. The plant illustrated by the artist has wilted flowers which have been shown with the ovary of a tulip. *Tulipa breyniana* could equally be one of two or three other species of *Homeria*, e.g., *H. ochroleuca* or *H. comptonii*.

The combination *Homeria collina* is usually attributed to Ventenat, who described the genus in 1808. This is incorrect (Milne-Redhead, 1937). The combination was actually made by Salisbury in 1812, the first author to adopt Ventenat's genus.

SOUTH AFRICA. CAPE: 33.18 (Cape Town): Near Cape Town (CD), *Thunberg s.n.* (Herb. Thunberg 1209, UPS); *MacOwan s.n.* (Herb. Norm. Austr. Afr. 252) (G, SAM). Table Mt., *Thode 8532* (STE); *Schlechter 1032* (GRA, Z). Groot Schuur, *Wolley Dod 593* (BOL). Wynberg Hill, *Pillans 10164* (MO). E slopes of Devils Peak, *Pillans 10424* (MO). Camps Bay, *Cassidy 290* (NBG). Clifton, *Goldblatt 4800* (MO, WAG). Sea Point, *Smith 2902* (PRE). Paarl Mountain (DB), *Kruger M36* (PRE). Stellenbosch flats (DD), *Garside 264* (K); *Bos 320* (PRE, STE). Jonkershoek Valley, *Bos 196* (WAG).

33.19 (Worcester): Bains Kloof, top of pass (CA), *Martin 2077/36* (NBG). Worcester end of Du Toits Kloof, *Barker 8026* (NBG); *Goldblatt 4701* (MO). Bo-Hermon-Wellington, *Goldblatt 3988* (BR, MO, PRE, WAG).

34.18 (Simonstown): Klaasenbosch (AB), *Zeyher 4125* (SAM). Kogelfontein, *Salter 8441* (SAM). Chapmans Peak lookout, *Goldblatt 500* (BOL). Above Ocean View, Kommetjie, *Goldblatt 4123A* (K, MO, PRE, WAG). Hout Bay, *White 5090* (PRE). Kalk Bay, along Boyes Drive, *Goldblatt 2132* (MO, NBG, PRE, WAG). Bergvliet Farm, *Purcell s.n.* (SAM, STE). Ladies Mile, Bergvliet, *Purcell s.n.* (MO, SAM-93364); Valley road, Hout Bay, *Goldblatt 4970* (MO).

34.19 (Caledon): foot of Houw Hoek Pass (AA), *Goldblatt 4004* (MO).

Unknown locality: Swartland, *Zeyher s.n.* (SAM 20639).

17. **Homeria minor** (Ecklon) Goldbl., comb. nov.—FIG. 20.

Moraea minor Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 15. 1827. TYPE: South Africa, Cape, sandy places in vineyards on the eastern slopes of Table Mt., *Ecklon Irid 7* (S, lectotype).

Vieusseuxia curvata Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 15. 1827. TYPE: South Africa, Cape, vineyards at Witteboom, *Ecklon s.n.* (S, lectotype).

Homeria rhopalocarpa Schltr., Bot. Jahrb. Syst. 27: 95. 1900. TYPE: South Africa, Cape, Windhoek, sandy soils, Vanrhynsdorp dist., *Schlechter 8336* (B, lectotype; BOL, C, E, G, GRA, K, M, MO, P, PRE, S, US, isolectotypes).

H. framesii L. Bolus, J. Bot. 69: 259. 1931. TYPE: South Africa, Cape, near Moorreesburg, *Ross Frames s.n.* (BOL-19147, lectotype; K, PRE, isolectotypes).

Plants 10–20(–30) cm high. *Corms* ca. 10 mm in diameter. *Leaf* inserted well above ground level, linear, channeled, exceeding the stem, 4–8 mm wide. *Stem* flexed above the leaf insertion and nodes, the main axis with only two internodes above the leaf, the lowermost node bearing a stem bract, sometimes with a short lamina, and leaflike, often 1–3 branched. *Spathes* initially ca. 5 cm long with the outer about two-thirds the inner, but the inner usually much elongating and enclosing the developing capsules, often reaching 7–8 cm. *Flowers* usually dark pink with a yellow nectar guide outlined in green, occasionally yellow, the tepals forming a narrow cup including the stamens and style branches, the upper part

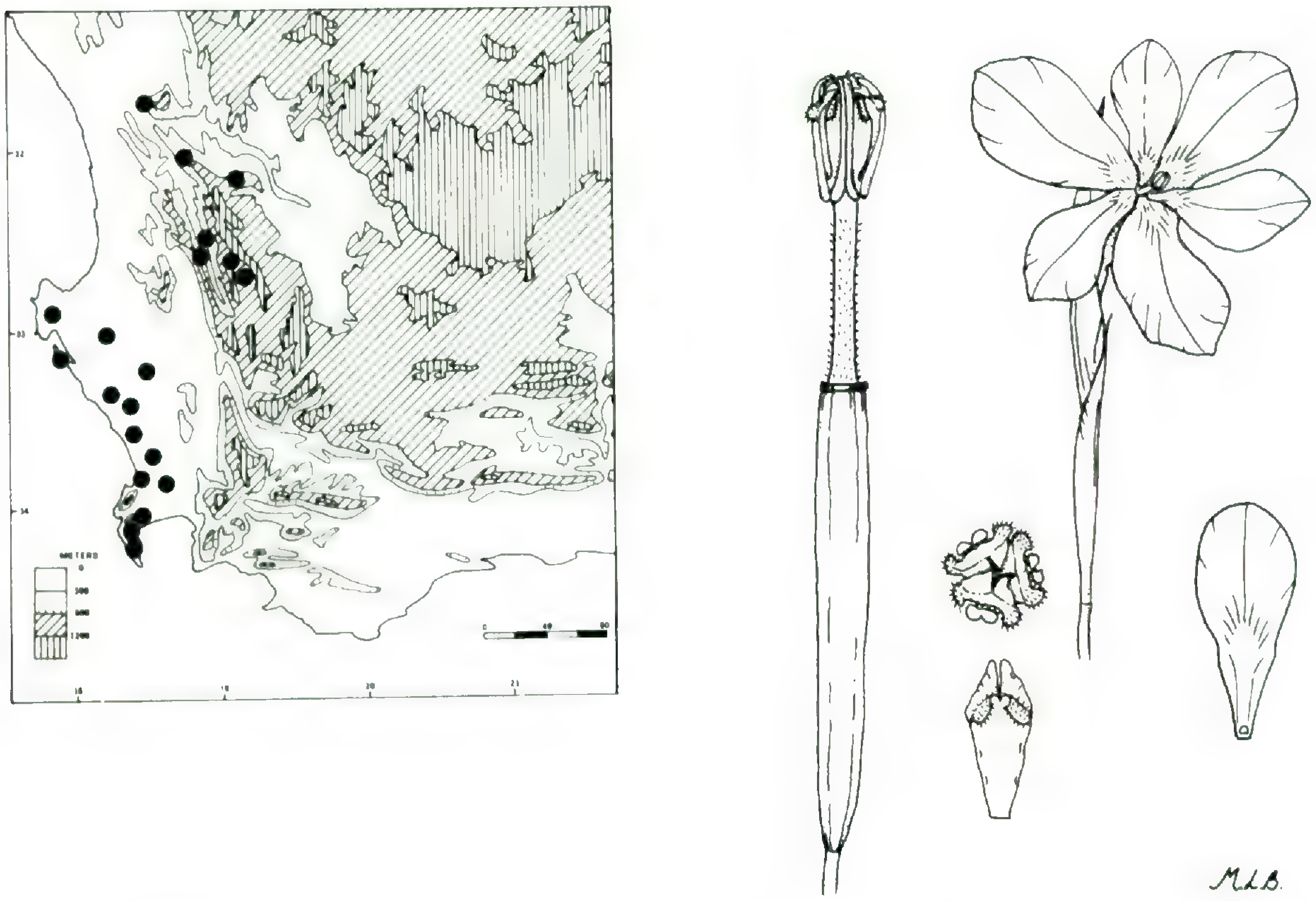

FIGURE 20. Floral morphology and distribution of *Homeria minor*. Flower and outer tepal ×1; ovary, stamens and style branches ×3; top view and single style branch ×5.

of the anthers sometimes exserted; *outer tepals* 21–37 mm long, the claw 10 mm long, suberect, the limb horizontal, 9–16 mm wide, obovate; inner tepals 20–36 mm long, 8–14 mm wide, often twisted. *Filaments* united, the column 6–9 mm, cylindrical, minutely pubescent in the lower half; *anthers* erect 3–5(–6) mm long, diverging in the upper half. *Ovary* 9–15 mm long, enclosed in the spathes; *style* branching towards the midline of the anthers; *branches* erect, barely diverging, 2–3 mm long, usually reaching the apex of the anthers, sometimes shorter, the stigma curved over the anther apex, with short, erect crestlike appendages less than 1 mm long. *Capsule* cylindrical, 25–28 mm long, without a beak, enclosed in spathes in younger stages. *Chromosome number* $2n = 12$.

Flowering time: mid August–September.

Distribution: west coast from the Cape Peninsula north into the Olifants River valley and extending locally into Elands Kloof; sandy soils; Fig. 20.

Homeria minor, better known by the later synonym *H. framesii*, is a relatively common species of the sandveld area between Cape Town and Saldanha Bay. It has not previously been realized that its distribution is considerably wider. It occurs on the Cape Peninsula, where it is usually confused with *H. collina*, and north along the west coast and in the Olifants River valley, where the type collection of *H. rhopalocarpa*, another synonym, was made.

The species is diploid, $2n = 12$, unlike the related *H. collina*, $2n = 24$, and is autogamous. The flowers are fugaceous, opening in the late morning and fading in mid afternoon of the same day. It is related both to *H. collina* and to *H. longistyla*. On the Cape Peninsula, where both *H. collina* and *H. minor* occur,

the species are separated by a difference in flowering times, although they are often sympatric and have similar soil preferences. *Homeria minor* flowers in late August and September here, while *H. collina* blooms from June onwards and is usually in seed by August.

Homeria minor can be distinguished from *H. collina* in fruit, but less easily in flower. It is usually a shorter plant, with a short ovary, long filaments, 6–9 mm, and anthers 3–5 mm long. The capsules are usually 20–25 mm, rarely to 28 mm long, and have no beak. *Homeria collina,* in contrast, has filaments 6–7 mm long, anthers 5–6 mm long, an ovary 14–19 mm long, and the beaked capsules are usually over 30 mm long. *Homeria minor* is closely allied to *H. longistyla* which occurs east of the range of *H. minor* and usually on clay or rocky ground. The differences between these two species are discussed under *H. longistyla.*

South Africa. cape: 31.18 (Vanrhynsdorp): Windhoek (DC), *Schlechter 8336* (B, BOL, C, E, G, GRA, K, M, MO, P, PRE, S, US). Nardouwsberg, at top of pass, *Goldblatt 2190* (M, MO, PRE), *3856* (MO, PRE).

32.17 (Vredenburg): slopes N of Vredenburg (DD), *Hutchinson 234* (K).

32.18 (Clanwilliam): Greys Pass (DB), *Steyn 632* (NBG). Olifants R. valley near Citrusdal turnoff, *Goldblatt 3239* (C, MO, PRE, WAG). 5 mi N of Citrusdal, *Leighton 1094* (BOL); *Lewis 1633* (SAM).

32.19 (Wuppertal): 4 km E of Klipfonteinrand (AA), *Nordenstam & Lundgren 1113* (MO, S). Elands Kloof (CA), *Lewis s.n.* (BOL as Nat. Bot. Gard. 2023-36).

33.18 (Cape Town): Donkergat Peninsula, foot of Postberg (AA), *Goldblatt 4085A* (K, MO). Koperfontein-Hopefield (AB), *Lewis 3565* (SAM). Near Hopefield, *Bachmann 1180* (M). Mamre-Darling (AD), *Davis s.n.* (SAM-60189). Mamre-Ysterfontein, *L. Bolus s.n.* (BOL-31567). Mamre hills, *Barker 4605* (NBG). Moorreesburg (BA), *Ross Frames s.n.* (BOL-19147, K, PRE). Near Mamre (CB), *Esterhuysen s.n.* (NBG). Cape Town-Mamre, milestone 32, *Esterhuysen 2938* (BOL). Mamre, *Lewis 99* (SAM). Koeberg (DA), *Goldblatt 3823* (MO, WAG). Killarney Industrial Park, Cape Town (DC), *Goldblatt 4830* (MO). Flats near Bellville, *Wall s.n.* (LD).

34.18 (Simonstown): Red Hill (AB), *Wolley Dod 3010* (BOL, K). Klein Slangkop, *Wolley Dod 3304* (K). Simons Bay, *Wright 272* (GH, K). Kalk Bay Mt., above Boyes Drive, *Goldblatt 4098* (MO, NBG, PRE, WAG). Near Ocean View, Kommetje, *Goldblatt 4124* (MO). Imhofs Gift, *Kies s.n.* (NBG-59090). Vineyards near Witteboom, *Ecklon s.n.* (S). Bergvliet farm, *Purcell s.n.* (SAM).

18. Homeria longistyla Goldbl., sp. nov. type: South Africa, Cape, near bridge over Riversonderend, E of Villiersdorp-Elgin road, *Goldblatt 4881* (MO, holotype; K, NBG, PRE, S, WAG, isotypes).—Fig. 21.

Planta 15–30 cm alta. Cormus 8–14 mm in diametro. Folium solitarium, supra terram insertum. Caulis flexuosus, aliquot ramosus, raro simplex. Spathae (3.5–)4–6 cm longae, exterior dimidia interior. Flores lutei vel subrosei, ungues tepalorum tubiformes, stamina inclusa; tepala exteriora 25–35 mm longa, ungue 11–15 mm, interiora parum breviora. Filamenta connata, 7–9 mm longa; antherae 4–7 mm longae, usitate contiguae. Ovarium 8–12(–15) mm longum; stylus divergens ad vel ultra apicem antherarum, rami breviores vel nulli.

Plants 15–30 cm tall. *Corms* 8–14 mm in diameter. *Leaf* solitary, inserted above ground level, linear, channeled, longer than the stem. *Stem* erect, flexed above the leaf insertion, usually with several branches, rarely simple, the stem bracts usually 3–5 cm long. *Spathes* (3.5–)4–6 cm long, the outer about half the inner. *Flowers* deep to pale orange-pink or pale yellow, with dark yellow nectar guides, the lower parts of tepals forming a cup 8–9 mm wide, including the filaments and anthers, the upper parts outspread, flaccid; *outer tepals* 25–35 mm long, the claw 11–15 mm, the limb 10–14 mm wide, more or less oblong, obtuse; inner tepals slightly shorter, narrower. *Filaments* united, 7–9 mm long, the column slender, cylindrical, minutely papillate-pubescent, smooth near the apex;

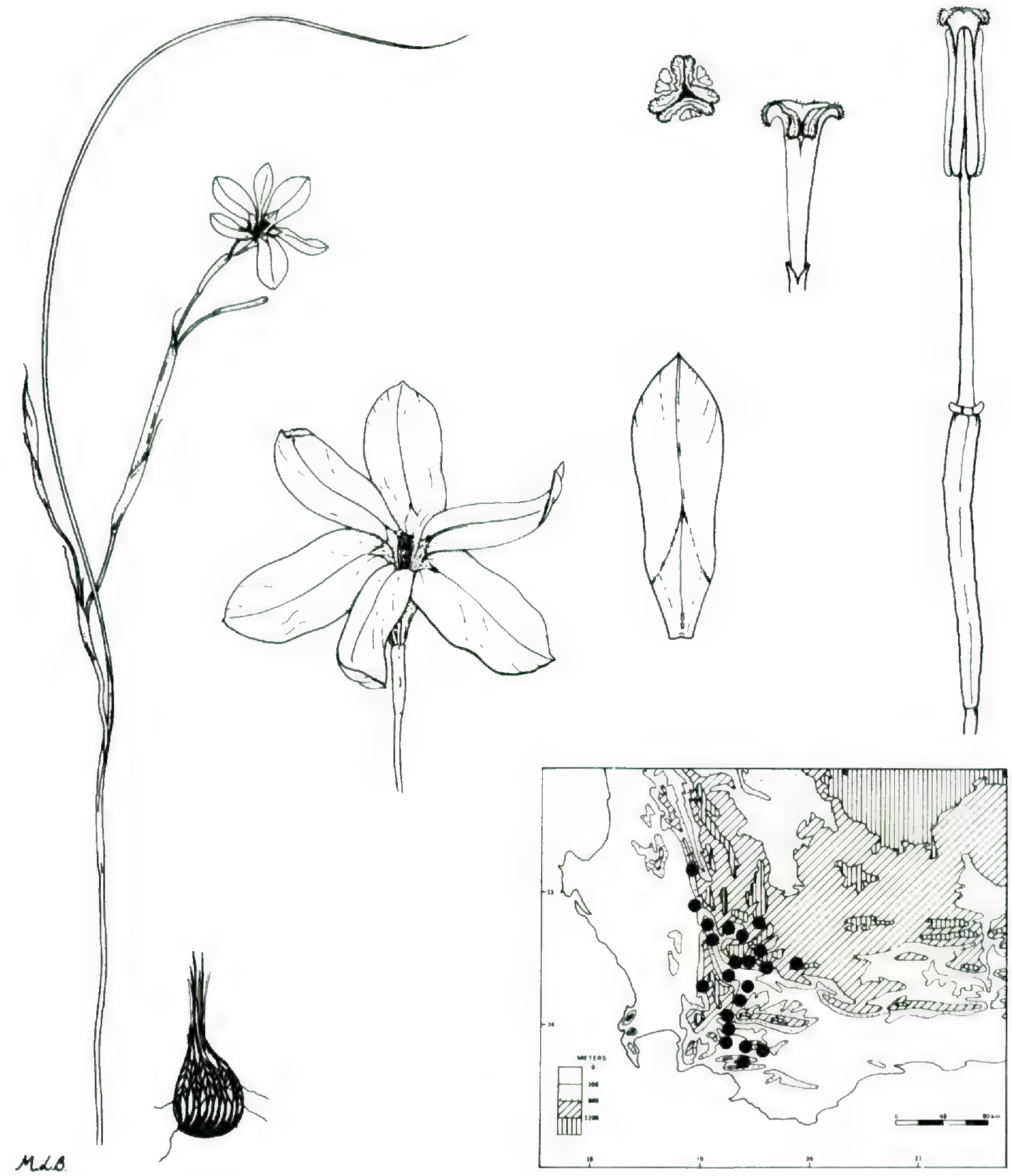

FIGURE 21. Morphology and distribution of *Homeria longistyla*. Habit ×0.4; corm, flower and outer tepal ×1; ovary, stamen and style branches ×3.

anthers erect, 4–6(–7) mm long, contiguous or slightly diverging in the upper third. *Ovary* 8–12(–15) mm long; *style* dividing near or beyond the apex of the anthers; *branches* short, 1–2 mm long or barely developed, the apices forming a bilobed stigma; crests minute, obscure, or lacking. *Capsule* 15–20 mm long, cylindrical, with a distinct short, acute beak ca. 1 mm long; seeds angled. *Chromosome number* $2n = 12$.

Flowering time: mid August–October.

Distribution: Caledon and Worcester districts, extending north to Ceres and Tulbagh and east to Koo and Montagu; clay soils in renosterbosveld; Fig. 21.

Homeria longistyla appears to be one of the most specialized species in the genus with the branching of the style almost or entirely suppressed. The style may divide near the apex of the anthers, with very short branches being produced, 1–2 mm long, or the style may essentially be undivided, with three apical stigmatic lobes. In other respects the species much resembles *H. collina* and particularly *H. minor,* to which it seems mostly closely related. The two can be distinguished when dry only by examination of the style which in *H. minor* divides at or below the midline of the anthers, and the well-developed style branches are fairly broad and at least 3 mm long with distinct crests. Also the ovary and capsules of *H. longistyla* are usually well exserted from the spathes, while those of *H. minor* are typically enclosed, at least during development, although the ripe capsules are usually exserted.

Homeria minor and *H. longistyla* have complementary distribution ranges. *Homeria minor,* found always in sandy soils, extends from the Cape Peninsula northward along the west coast into the Olifants River valley. *Homeria longistyla,* which grows on sand, but more often on clay soils, occurs on the slopes of the Olifants River Mountains and inland in the Tulbagh, Worcester, Caledon, and Ceres districts. Although *H. minor* and *H. longistyla* seem clearly to be very closely related, it seems reasonable and useful to recognize the two as they do not appear to intergrade and can readily be distinguished by careful attention to the critical style characteristics. The morphological distinction is supported by the reproductive biology of the two species. *Homeria longistyla* is a self-incompatible species while the several populations of *H. minor* studied have proved to be autogamous.

SOUTH AFRICA. CAPE: 33.19 (Worcester): Near Saron (AA), *Schlechter 4872* (B, BOL, C, GRA, K, M, SAM). Near Tulbagh Road Station (AC), *Goldblatt 4757* (MO). Prince Alfreds Hamlet (AD), *Lewis 2555* (SAM). Near Ceres, *Marloth 6184* (PRE). Hottentots Kloof (BA), *Barker 3019* (NBG). Lakenvlei (BC), *Barker 1319, 1320* (NBG). Top of Swaarmoed Pass, *Goldblatt 4413* (BOL, G, MO, PRE). Near Worcester (CB), *Leipoldt s.n.* (BOL-31598). Karoo Gardens, *Olivier 135* (PRE). Brandvlei, *Salter 6842* (BOL). Du Toits Kloof-Breede R., *Goldblatt 3918* (MO), *4708* (BR, MO, WAG). Foot of Fonteinjiesberg, Onse Rug farm, *Goldblatt 4209* (MO). Below Zebra Kloof Dam, *Goldblatt 4733* (K, MO, S). Klein Drakenstein Mts., S. Hugenot (CC) *Salter 4662* (BOL, K), French Hoek, Zachariashoek, *Haynes 373* (PRE). Stettyn (CD), *Leipoldt 3556* (BOL). Hex R. valley (DA), *Wolley Dod 4023* (BOL, K). Rabiesberg slopes, *Lewis s.n.* (BOL-31593). Near Koo (DB), *Goldblatt 4181* (MO). 2 mi E of Robertson (DD), *Acocks 16108* (PRE).

33.20 (Montagu): slopes of Kloof near Baths (CC) *Page 17* (PRE).

34.19 (Caledon): Eseljag-Queen Anne (AA), *Goldblatt 3999* (MO). 1 km E of bridge over Riviersonderend on Bot R. road, *Goldblatt 4881* (K, MO, NBG, PRE, S, WAG). W of Eseljag Pass, *Goldblatt 3998* (MO), *4736* (MO, PRE). Flats S of Villiersdorp toward Theewaterkloof Dam (AB), *Goldblatt 4012* (BR, MO, PRE, S). Boontjies Kraal, W. Caledon, *Creasy s.n.* (NBG-59206). Commonage, Caledon, on Zwartberg slopes, *Guthrie s.n.* (BOL-16921). Zwarteberg, Caledon, *Zeyher 4074* (P, PRE, S, SAM).

19. Homeria patens Goldbl., sp. nov. TYPE: South Africa, Cape, Clanwilliam distr., near Boontjies River, *Leipoldt s.n.* (BOL-20768, holotype; K, SAM isotypes).—FIG. 22.

Planta 25–45 cm alta. Tunici cormi nigri. Folium solitarium, raro dua, supra terram insertum. Spathae herbaceae 4–6 cm longae. Flores lutei vel aurantiaci, tepala extensa a basem, unguibus cupulatis laxe; exteriores 25–27 mm longae, ungues ca. 9 mm. Filamenta connata, columna 7–8 mm longa, papillosa infra; antherae ca. 4 mm longae. Ovarium 9–10 mm longae; stylus divergens ad apicem columnae filamentarum, rami 3–4 mm longi, cristae breves.

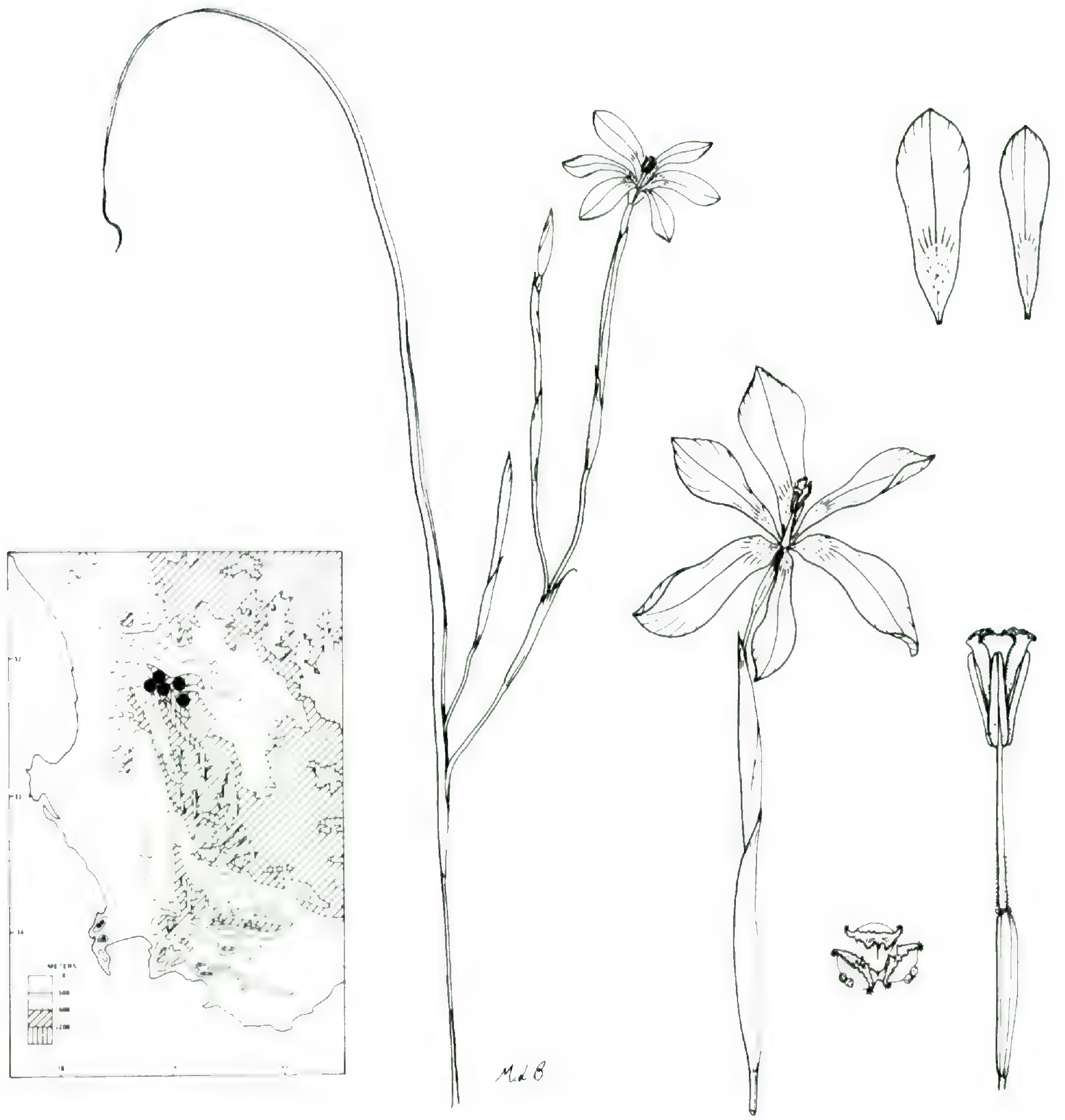

FIGURE 22. Morphology and distribution of *Homeria patens*. Habit ×0.5; flower, inner and outer tepal ×1; ovary, stamens and style branches ×2.5, the top view ×5.

Plants 25–45 cm high. *Corms* ca. 10 mm in diameter, the tunics black. *Leaf* solitary 1 (or rarely 2), linear, canaliculate, inserted well above ground, to 5 mm wide, much exceeding the stem. *Stem* erect, usually many branched, flexed above the leaf insertion, and above the stem bracts, the bracts 3–4 cm long. *Spathes* herbaceous, brown tipped, 4–6 cm long, the inner about twice as long as the outer, elongating somewhat as the capsules develop. *Flowers* bright yellow or orange, with dark yellow nectar guides, the tepals spreading from the base, the claws ascending and loosely cupped, the limbs outspread; *outer tepals* 25–27 mm long, the claw ca. 9 mm, pandurate, to 9 mm at the widest; inner tepals to 24 mm, narrower. *Filaments* united, cylindric, 7–8 mm long, papillate in the lower half; *anthers* ca. 4 mm long, diverging from the base. *Ovary* 9–10 mm long,

exserted; style dividing at the apex of the filament column; *branches* 3–4 mm long, about as wide as the anthers and reaching or slightly exceeding the anther apex; crests erect, very short (obscure in dry material). *Capsule* usually exserted or partly included in the spathes, 12–15 mm long. *Chromosome number* $2n = 12$.

Flowering time: mid August–September.
Distribution: sandy soils in valleys of the Pakhuis and Nardouw Mts.; Fig. 22.

Homeria patens is characterized by a rather open flower. The tepal claws incline gently upward forming a very open shallow cup that includes the filament column. The tepal limbs extend laxly outward, and the diverging anthers are held well above the flower cup. The species appears to be related to the more widespread and specialized *H. minor* but the two are quite distinct in flower structure. The narrow tepal cup and completely included filaments and anthers of *H. minor* are in fact starkly different when seen in living plants. *Homeria vallisbelli,* occurring to the north in the Nieuwoudtville district, is probably also closely allied. The latter differs in its well-formed tepal cup, reduced style branches, and enclosed ovary and capsules.

The record indicates that *H. patens* is rather uncommon and restricted to a few valleys on the east and west from the Pakhuis Mountains near Clanwilliam. Further collecting here may well extend its known range.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): 5 mi from Clanwilliam on Kranzvlei road (BB), *Gillett 4021* (BOL, K, MO). Nardouw Kloof, *Stokoe s.n.* (SAM-59807). Clanwilliam, *Leipoldt 235* (SAM).
32.19 (Wuppertal): Near Boontjies R. (AA), *Leipoldt s.n.* (BOL-20768, K, SAM). Brandewyn R., *Compton 7694* (NBG); *Barker 251, 252* (NBG); *Lewis s.n.* (BOL-22260). Flats east of Pakhuis Pass, *Goldblatt s.n.* (MO), *5159* (K, MO).

20. Homeria vallisbelli Goldbl., sp. nov. TYPE: South Africa, Cape, Oorlogskloof, *Schlechter 10947* (K, holotype; B, BOL, M, isotypes).—FIG. 23.

Planta 15–30 cm alta. Cormus 8–15 mm in diametro. Folium unicum supra terram insertum, caulem excedens. Caulis flexuosus, simplex vel aliquot ramosus. Spathae 3.5–5(–7) cm longae, interior longitudine circa duplo longior exteriore, postea elongata et fructus includens. Flores rosei vel flavi, ungues tepalorum cupulati; tepala exteriora 26 mm longa, limbis 16–18 mm, interiora parum breviora. Filamenta connata, 7–8 mm longa; antherae ca. 4.5 mm longae, divergentes. Ovarium 9–12 mm longum, inclusum, stylus divisus inter basem et medium antherarum, rami ca. 2.5 mm, bifurcati, cristae obscurae.

Plants 15–30 cm high. *Corms* 8–15 mm in diameter, the tunics black. *Leaf* linear, channeled, exceeding the stem, inserted well above ground level, the margins inrolled. *Stem* erect, flexed above the leaf insertion and above the sheathing part of the bracts, simple to several branched, the stem bracts 2.5–5(–8) cm long, the lowest occasionally ± leaflike. *Spathes* 3.5–5(–7) cm long, herbaceous, with brown attenuate apices, the inner initially about twice as long as the outer, later elongating to enclose the fruits. *Flowers* deep pink or pale yellow, with dark yellow nectar guides outlined in dark purple or green, the tepals forming a wide cup, ca. 8 mm deep and 10 mm wide at the apex, including the filament column, the tepal limbs spread horizontally; *outer tepals* 26 mm long, the limb 16–18 mm, obovate, widest just below the apex, the claw ca. 10 mm long, puberulous in the lower part; inner tepals slightly shorter and narrower. *Filaments* united, the column 7–8 mm long, slightly narrowed towards the apex, pubescent in the lower

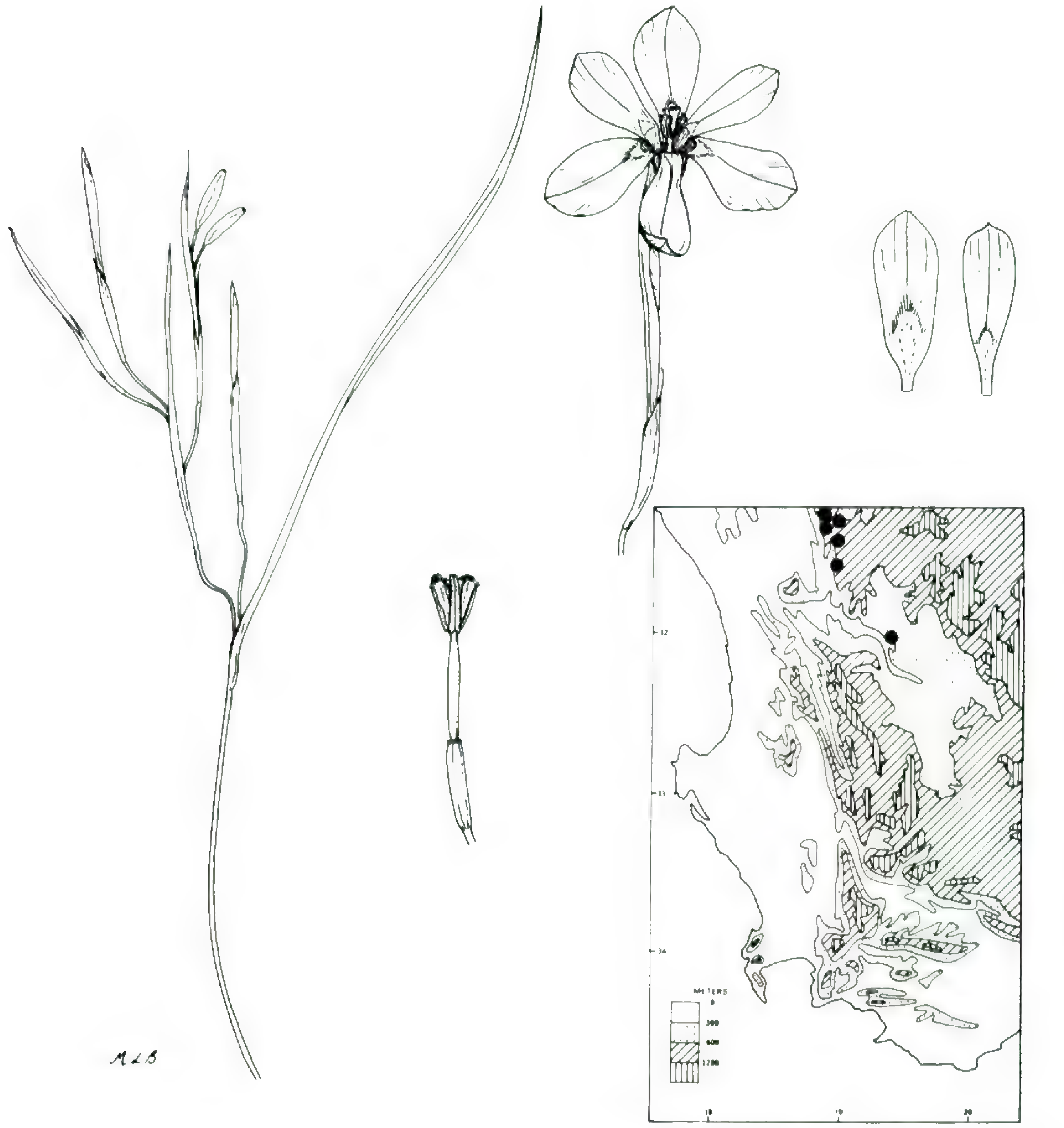

FIGURE 23. Morphology and distribution of *Homeria vallisbelli*. Habit ×0.5; flower and inner and outer tepal ×1; ovary, stamens and style branches ×2.

two-thirds; *anthers* ca. 4.5 mm long, diverging. *Ovary* 9–12 mm long, enclosed in the spathes, rarely partly exserted; *style* branching between the base and the middle of the anthers; *branches* narrow, ca. 2.5 mm long, bilobed, receptive at the tips of the lobes, reaching to near the apex of the anthers; crests obscure, shorter than the stigma lobes. *Capsule* cylindric, to 14 mm long, usually completely enclosed in the spathes. *Chromosome number* $2n = 12$.

Flowering time: (late July–)August–September.

Distribution: western part of the Calvinia district, especially common around Nieuwoudtville, and extending south with an outlying population recorded from Blinkvlei in the Doorn River basin; mainly on sandy soils, or in very rocky sites; Fig. 23.

The earliest collections I have seen of *Homeria vallisbelli* are those of Schlechter, collected in 1897 (*Schlechter 10947,* Oorlogskloof). Evidently Schlechter considered this a new species for the collection bears the name *H. tulipifera.* One of the sheets of this collection at the Berlin herbarium has the inscription "*typus auct.*" The species was however never described.

The specific epithet *vallisbelli* is derived from the name Oorlogskloof, one of the first farms in the Nieuwoudtville vicinity, and the name sometimes given in the past to the general area around Nieuwoudtville.

This species is apparently related to the more widespread *H. minor* of the Cape west coast and Olifants River valley, and the two are easily confused, especially when dried. However, *H. vallisbelli* differs in several important ways. First, the tepal cup is fairly wide and encloses only the filaments, while in *H. minor* a narrower cup encloses the anthers as well. Second, the short style branches are entirely without crests, where *H. minor* has short but clearly visible crests. Third, the ovary is usually entirely enclosed in the spathes, the inner of which elongates during fruit development, to completely enclose the capsules (which occasionally become partly exserted when ripe). In *H. minor* the ovary is often enclosed at flowering time or partly exserted, but the ripe fruits are usually exserted from the spathes. The species is diploid, but in contrast with *H. minor,* which is autogamous, plants of the single population of *H. vallisbelli* grown experimentally were self-incompatible.

South Africa. cape: 31.19 (Calvinia): Nieuwoudtville (AC), *Loubser 952* (NBG); *Marloth 7803* (PRE). Oorlogskloof hills, *Schlechter 10947* (B, BOL, GRA, M). Between Oorlogskloof and Nieuwoudtville, *Leipoldt 3852* (BOL, K, PRE). Nieuwoudtville-Van Rhyns Pass, *Lewis 1997* (SAM). Nieuwoudtville-Grasberg road, *L. Bolus s.n.* (BOL-21068, SAM); Grasberg farm, *Lavranos 10908* (MO). 3–4 mi W of Nieuwoudtville, *Lewis 2275* (PRE, SAM); *Barker 6477, 6479, 6481* (NBG). 4.4 mi S of Nieuwoudtville, *Thompson 363* (K, STE). Oorlogskloof-Papkuilsfontein, *Leipoldt 3012* (BOL), *3013* (BOL, K). Nieuwoudtville waterfall *Goldblatt 3952* (K, MO). Lokenberg (CA), *Acocks 17023* (K).

32.19 (Wuppertal): Between Blinkvlei and Doorn R. (BA), *Lewis 5822* (NBG).

21. Homeria flavescens Goldbl., sp. nov. type: South Africa, Cape, Cedarberg, at turnoff to Krom River farm, *Goldblatt 4058a* (MO, holotype; NBG, isotype).—Fig. 24.

Planta 12–30 cm alta. Cormus 8–12 mm in diametro. Folium unicum, supra terram insertum, ad 4 mm latum. Caulis flexuosus, ramosus. Spathae 3–6 cm longae, interior circa duplo longior exteriore, postea elongata et capsulas juvenes includens. Flores pallide flavescentes, ungues tepalorum cupulati, includentes columnam filamentarum; tepala exteriora 16–24 mm longa emarginata, interiora parum breviora. Filamenta connata interdum libera in parte superiore; antherae 3–4 mm longae, divergentes. Ovarium 7–12 mm longum, rami styli ca. 2 mm longi, bifurcati, quam antheris breviores.

Plants small to medium, (12–)15–30 cm high. *Corm* 8–12 cm in diameter, the tunics black. *Leaf* solitary, inserted well above ground, channeled, linear to 4 mm wide, much exceeding the inflorescence, trailing. *Stem* erect, strongly flexed above the leaf insertion, several to many branched, the bracts 3.5–5.5 cm long. *Spathes* 3–6 cm long, the inner initially about half the outer but later elongating to enclose developing fruits. *Flowers* pale yellow with deep yellow nectar guides edged in gray, the lower part of the tepals forming an open cup, 8 mm at the mouth from which only the upper part of the filament column emerges, the tepals spread horizontally above; *outer tepals* 16–24 mm long, 7–9 mm wide, emargin-

FIGURE 24. Morphology and distribution of *Homeria flavescens*. Habit and corm ×0.5; flower ×1; ovary, stamens and style branches ×2, the detail of the style branches much enlarged.

ate, the claw 5–6 mm long, the limb oblong, or narrowed in the lower third; *inner tepals* 17–19 mm, narrower. *Filament* column ca. 5 mm long, sometimes free in the upper 0.5–2 mm, minutely papillate; *anthers* 3–4 mm long, diverging. *Ovary* 7–12 mm long, enclosed in the spathes; *style* dividing at the base of the anthers; *branches* ca. 2 mm long, flat, deeply bilobed, shorter than the anthers, the lobes stigmatic at the apices and held between the anthers. *Capsule* 8–16 mm long, oblong to cylindric, enclosed until maturity. *Chromosome number* $2n = 9$.

Flowering time: September; flowers open in early morning and fade between 1 and 2 P.M.

Distribution: mountains of the west coast from the Southern Cedarberg to the Giftberg; in sandy soil, with dry fynbos; Fig. 24.

Homeria flavescens is a poorly known species which is apparently distributed widely in the mountains of the west coast, from the Southern Cedarberg to the Giftberg. It is rather variable as circumscribed here, and includes forms in the south (*Goldblatt 4058a, Goldblatt 5669*) with small flowers and somewhat larger-flowered forms in the north (*L. Bolus s.n.*). The latter specimens bear the manuscript name *H. klawerensis* L. Bol. The species is characterized by its very pale yellow flowers with emarginate outer tepals, diverging, flat style branches which are shorter than the anthers, and a wide tepal cup.

The habitat of *H. flavescens* appears to be flats and mountain slopes with sandy, and often very thin soil overlying sandstone rock. It grows in dry fynbos and flowers best in open places away from other vegetation. The places where I have seen the species had not been recently burnt.

Three populations have been examined cytologically to date, all from the southern Cedarberg where three adjacent populations have $2n = 9$, a most unusual situation. The latter karyotype consists of three metacentrics and six acrocentrics, and thus 12 major chromosome arms which correspond to the 12 acrocentric chromosomes of the typical basic *Homeria* karyotype. The $2n = 9$ karyotype has also been found in *H. tenuis* (also $2n = 10$ and 8) which coincidentally has a similar range. *Homeria tenuis* may be closely related but is clearly quite distinct, having much smaller flowers of slightly different structure in which the proportionately similar tepal claws form a narrow cup round the lower half of the filament column.

SOUTH AFRICA. CAPE: 31.18 (VanRhynsdorp): Klawer (DC), *Lewis 2008* (SAM); *L. Bolus s.n.* (BOL-21313, K).
32.19 (Wuppertal): Dwars Rivier-Krom Rivier turnoff (CB), *Goldblatt 4817* (MO). Cedarberg, at Krom Rivier turnoff, *Goldblatt 4058a* (MO, NBG). Krom Rivier farm, *Goldblatt 5669* (MO, NBG).

22. **Homeria tenuis** Schltr., Bot. Jahrb. Syst. 27: 95. 1900. TYPE: South Africa, Cape, Pakhuis Mts., *Schlechter 8647* (B, lectotype; BOL, E, G, GRA, K, MO, P, PRE, US, Z, isolectotypes).—FIG. 25.

Plants usually small, 7–20 cm high. *Corms* 5–10 mm in diameter, the tunics black or brown, sometimes soft textured. *Leaf* solitary, inserted well above ground, channeled, linear-filiform, to 3 mm wide, exceeding the inflorescence. *Stem* erect, sharply flexed above the leaf insertion, few to several branched, the branches flexed above the stem bracts, the bracts 15–30 mm long. *Spathes* 2–4(–6) cm long, inner initially twice the outer, but later elongating in fruit to partly enclose the immature fruits. *Flowers* pale to deep yellow, small, the lower part of the tepals suberect, forming a cup ca. 3 mm long around the lower half of the filament column, the tepals spreading above; *outer tepals* 10–12 mm long, the claw 2–3 mm long, the limb oblong, to 6 mm wide; inner tepals slightly shorter, to 4 mm wide, lanceolate. *Filaments* united, the column smooth, cylindrical, 5–6 mm long; *anthers* 1.5–2 mm long, diverging from the base, collapsing after anthesis. *Ovary* 5–8 mm long, enclosed in the spathes; *style* branching at the

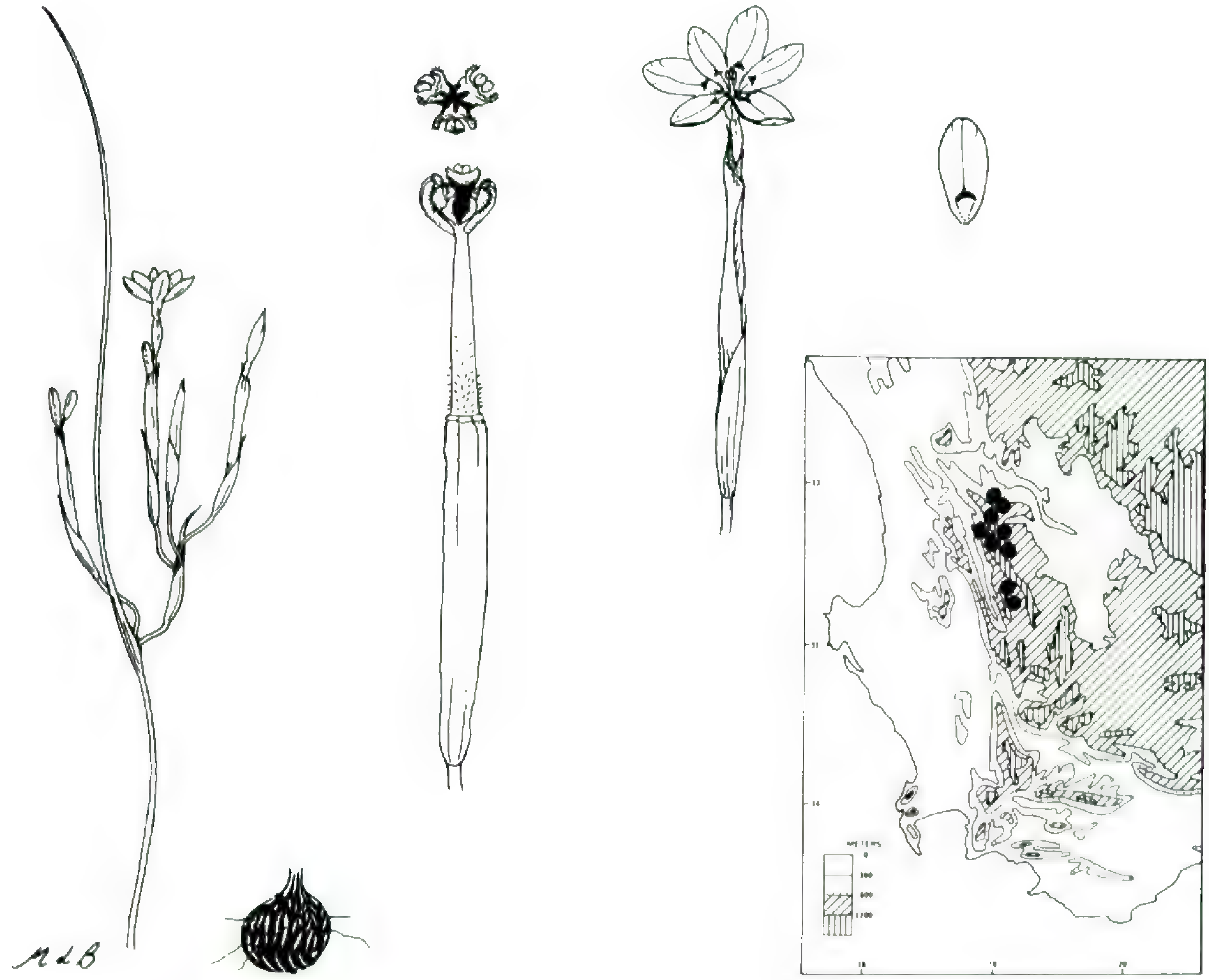

FIGURE 25. Morphology and distribution of *Homeria tenuis*. Habit ×0.5; corm, flower and inner tepal ×1; ovary, stamens and style branches ×5.

base of the anthers; *branches* 1.5–2 mm long, flattened, the stigma bilobed, reaching the mid to upper part of the anther, receptive on the inner lateral surfaces; crests usually present, erect, very short, usually obscured by the anthers. *Capsule* 8–11 mm long, included in the spathes until ripe, clavate-cylindric. *Chromosome number* $2n = 10, 9, 8$.

Flowering time: mid August–early October; flowers open in the afternoon after 2:30 and fade towards evening.

Distribution: Cold Bokkeveld and Cedarberg Mountains, between Elands Kloof and Pakhuis Pass; shallow sandy soils, often on rock ledges and flushes; Fig. 25.

Homeria tenuis is one of the dwarf species of *Homeria*, and its flowers are the smallest in the genus. Its range is centered in the Cedarberg Mountains, with the northernmost record at Brandewyn River, east of Pakhuis Pass, and the southernmost in Elands Kloof. A record from Piketberg [*Van Zyl s.n.* (BOL)] is doubtful. It grows in sandy, often very shallow soil overlying rock or in rock cracks, and in very extreme conditions plants are particularly dwarfed. In deeper soil plants tend to be taller and more branched but do not have significantly larger

flowers. The growth of *H. tenuis* is strongly inhibited by surrounding vegetation, and it flowers best after fires or when areas have been cleared of bush.

Cytologically the species is of considerable interest as available counts have revealed three populations with $2n = 10$, one with $2n = 8$, and several with $2n = 9$. The latter number, $2n = 9$, has also been recorded in the related *H. flavescens,* which also has $2n = 12$. These two species contrast sharply with the basic $x = 6$ found in all other species of the genus except the unrelated *H. pallida,* a form of which has $2n = 8$. *Homeria tenuis* is evidently an aneuploid species. The significance of three different chromosome numbers in this species has yet to be explained. Plants from the two populations grown experimentally have proved to be autogamous.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): Pakhuis Pass (BB), *Salter 7519* (SAM); *Stokoe s.n.* (SAM-55679); *Compton 4312* (BOL); *DeVos 1669* (STE); *Esterhuysen 5023* (PRE). Clanwilliam, *LeRoux s.n.* (BOL). Piketberg (DC), *Van Zyl s.n.* (cult.) (BOL).

32.19 (Wuppertal): Pakhuis-Brandewyn R. (AA), *Goldblatt 3882* (MO, NBG, S). Pakhuisberg, *Schlechter 8647* (B, BOL, E, G, GRA, K, MO, P, PRE, US, Z). Boontjies R., E of Pakhuis, *Leipoldt 20767* (BOL). Heuningvlei, *Esterhuysen 8060* (BOL). Uitkyk Pass (AC), *Barker 266* (NBG); *Lewis s.n.* (SAM-52414). Top of Uitkyk (Cedarberg) Pass, *Martin s.n.* (NBG-59220); *Gillett 4088* (BOL, K, PRE); *Goldblatt 4056* (MO). Welbedacht Kloof, *Stokoe s.n.* (SAM-55680). Driehoek road, Matjes R. valley, *Goldblatt 5122* (K, MO, PRE, S), *5674* (MO). Eikeboom, Cedarberg, *Leighton s.n.* (BOL-21505, PRE). Old Elands Kloof Pass (CA), *Thompson 2951* (STE); *Barker 3116* (BOL, NBG); *Compton 17324* (NBG). Top of Elands Kloof, *Lewis 1350* (SAM); *Goldblatt 5246* (MO, NBG). Krom R. Kloof (CB), *Esterhuysen 20546* (BOL, PRE). Krom River farm, *Goldblatt 5668* (MO).

23. Homeria miniata (Andr.) Sweet, Brit. Flow. Gard. 2: *tab. 152.* 1826. Baker, Fl. Cap. 6: 29. 1896.—FIG. 26

Moraea miniata Andr., Bot. Repos. *tab. 404.* 1804. TYPE: South Africa, Cape, exact locality unknown, illustration in Andr. Bot. Repos. *tab. 404.*

Homeria lineata Sweet, Brit. Flow. Gard. 2: *tab. 178.* 1826. TYPE: South Africa, Cape, exact locality unknown, illustration in Brit. Flow. Gard. *tab. 178.* Baker, Fl. Cap. 6: 28. 1896.

Moraea lineata (Sweet) Steud., Nom. Bot. 2: 160. 1840.

M. gigantea Klatt, Linnaea 35: 381. 1868. TYPE: South Africa, Cape, "near Little Quaggasfontein," *Burchell 1431* (K, lectotype). South Africa, "between Great and Little Reed Rivers," *Burchell 1388* (K, syntype).

Homeria albida L. Bolus, J. Bot. 69: 258. 1931. TYPE: South Africa, Cape, between Van Rhynsdorp and Van Rhyns Pass, *L. Bolus s.n.* (BOL-19353, holotype; K, isotype).

Plants medium to large, 15–60 cm tall. *Corms* 1–2.5 cm in diameter, with a few to many cormlets round the base, the tunics black, reticulate. *Leaves* (2–)3, linear, canaliculate, (4–)8–12(–17) mm wide, the lowermost basal, the others cauline. *Stem* straight or slightly flexed above the bracts, the branches short, upright, the stem bracts 3–4.5(–6) cm long. *Spathes* (3–)4–6 cm long, the outer about two-thirds the inner, the apices brown. *Flowers* pink, yellow or white, with triangular yellow nectar guides dotted with green, the tepals with a short erect claw, ca. 2 mm long, appressed to the filament column, the limb outspread; *outer tepals* 13–22(–27) mm long, the claw narrow, 2 mm long, pubescent above the midline, the limb 6–10 mm wide, ovoid-ellipsoid; inner tepals smaller, ellipsoid-obovoid. *Filaments* united, the column 6–8 mm long, narrow at the base, swollen abruptly and then tapering gradually to the apex, the bulbous part pubescent; *anthers* ca. 2 mm long, after anthesis ca. 1.5 mm, erect, contiguous. *Ovary* 5–10 mm long; *style* dividing just above the anther base; *branches* short, obscured by the an-

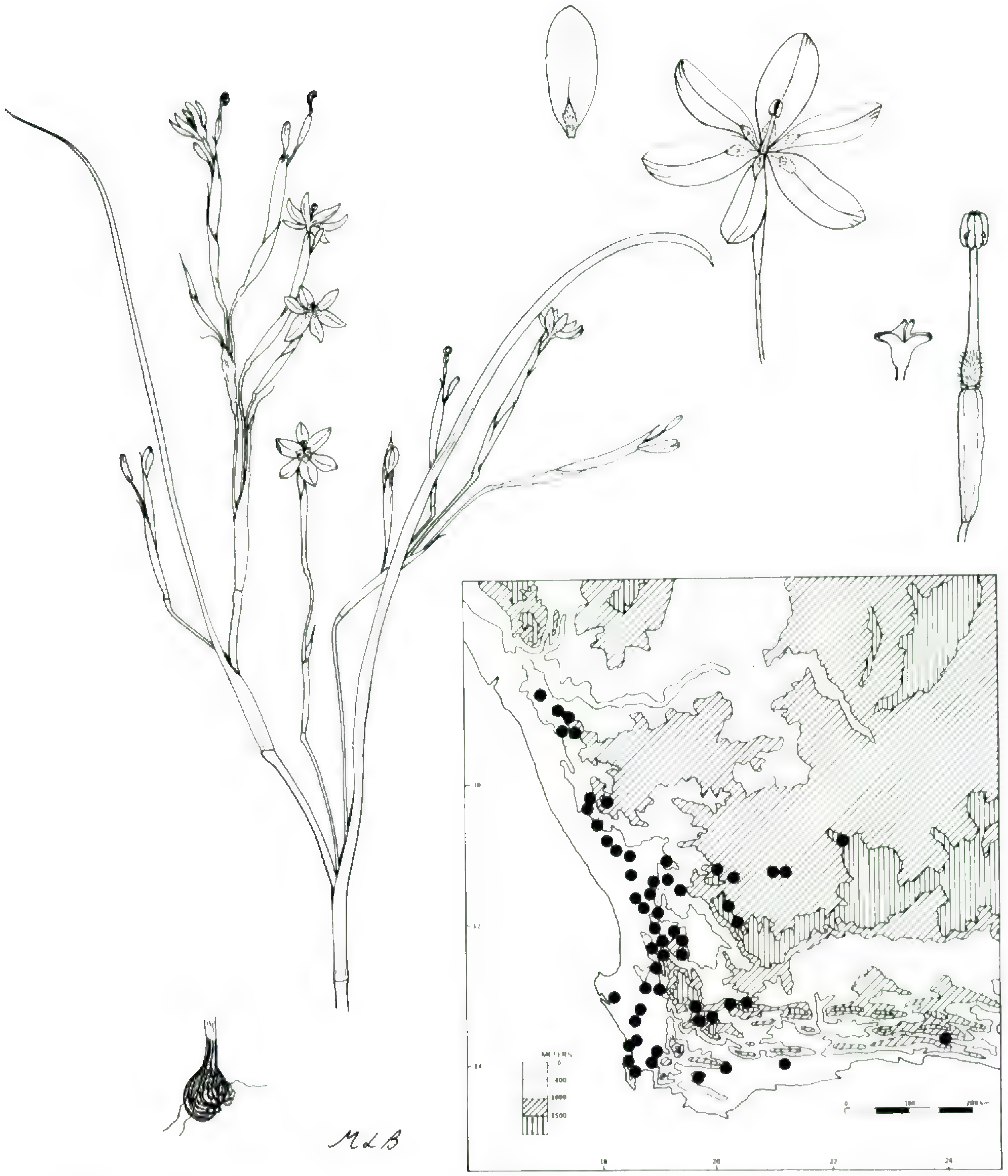

FIGURE 26. Morphology and distribution of *Homeria miniata*. Habit ×0.3; corm, flower and inner tepal ×1; ovary, stamens and style branches ×3, the separated style branches much enlarged.

thers, deeply forked, the arms slender, stigmatic apically and emerging between the anthers; crests absent. *Capsule* 12–16 mm long, cylindrical-ellipsoid; *seeds* angled. *Chromosome number* 2*n* = 12 (2*n* = 18, 24 recorded in weedy plants of pastures and cultivated land).

Flowering time: July–September(–October).

Distribution: common along the west coast as far north as Steinkopf and in the western Karoo, occasional in the southern Cape; mainly in clay soils; Fig. 26.

Homeria miniata is one of the most common and the most widespread species of *Homeria*. It extends from the Cape Peninsula north to Namaqualand and inland to Touws River, the Roggeveld and Hantamsberg. Plants vary in flower color from salmon pink to pale yellow, to occasionally pure white. Most often populations are uniform in color. Pink flowers occur predominantly in the south, but from Klawer northwards yellow flowers become increasingly common. White flowers are rare, and are found in populations scattered in Namaqualand and between Van Rhyns Pass and Van Rhynsdorp (the type area for the synonym *H. albida*). A distinctive form also grows at the foot of the Cedarberg, Nardouw and Matsikamma mountains; this form has somewhat smaller and deeper pink flowers.

The species prefers clay soils, although in Namaqualand it often occurs on the gritty granite-derived sand of the area. It has not been recorded growing on sandstone-derived soils. *Homeria miniata* has become a serious weed, and in the south it is often difficult to tell wild from adventive populations, the latter obvious on road verges and in overgrazed pastures. It reproduces readily from axillary cormlets and eradication is very difficult. Some forms in old fields are obviously sterile, and these produce much larger numbers of cormlets than the wild plants. Causes of sterility appear to be chromosomal abnormalities, such as triploidy and aneuploidy, as seen in two populations near Stellenbosch, which I have investigated.

Homeria miniata is related to a group of species with very similar to identical flowers and outspread limbs.

It can readily be distinguished from close allies by its two or usually three straight, linear leaves, and the much swollen and pubescent base of the filament column.

SOUTH AFRICA. CAPE: 29.17 (Springbok): Steinkopf (BA), *Salter 3752* (BOL); *Marloth 6764* (PRE). 4 mi W of Steinkopf, *Hall 115* (WAG). 15 mi N of Springbok (BD), *Maguire 441* (NBG). Nigramoep (DA), *Wikner s.n.* (SAM-65668). Top of Spektakel Pass, *Thompson 1041* (STE). 2 mi E of Springbok (DB), *Compton 22050* (NBG). Hester Malan Reserve, *LeRoux 905, 770* (PRE).

30.17 (Hondeklipbaai): Grootvlei (BD), *Compton 6611* (NBG); *Lewis 5471* (NBG). Upper Bowesdorp valley, *Pillans s.n.* (BOL-31550). Bowesdorp, *Stokoe s.n.* (SAM-55655). Kamieskroon, *Goldblatt 3672A* (MO), *116* (J), *Lewis 5473* (NBG). 7 mi S of Kamieskroon (BD), *Salter 3809* (BOL, K). Brakdam, *Compton 17206* (NBG).

30.18 (Kamiesberg): Kamiesberg (AC), *Martin s.n.* (NBG-59237). Leliefontein, *Rodin 1460* (BOL, K, MO, PRE, S, US). Kamiesberg, top of Studers Pass, *Goldblatt 4045* (MO, PRE). Between Garies and Bitterfontein at Swart Doorn R. (CC), *Lewis 1377* (SAM).

30.22 (Carnarvon): 3.5 mi SW of Carnarvon (CC), *Acocks 16413* (K, PRE).

31.18 (Van Rhynsdorp): Nuwerus (AB), *Steyn 476* (NBG); *Compton 3727* (NBG); *Barker 3619* (NBG). 2 mi S of Nuwerus, *Lewis 1378* (SAM). Bitterfontein, *Compton 11354* (NBG). Knersvlakte (B), *Compton 20689* (NBG); *Pillans 6344* (BOL, K). Knersvlakte near Vars R. (BC), *Goldblatt 3679* (MO). 12 km S of Van Rhynsdorp (DA), *Goldblatt 3886* (C, MO, S, WAG). Zandkraal, *Barker 5636, 5637, 5658* (NBG). Wiedow R., *Lewis 2276* (SAM). Grootdrif, SW of Van Rhyns Pass (DB), *Goldblatt 2284* (MO, PRE). Grootdrif-Van Rhyns Pass, *Goldblatt 3887* (MO, US, WAG). Windhoek (DC), *Schlechter 8356* (BOL, E, G, GRA, K, MO, P, PRE, SAM, S, US, Z). Katberg Pass, Matsikamma plateau (DD), *Goldblatt 3849* (BOL, C, MO, PRE, S, US, WAG).

31.19 (Calvinia): Brandkop, N of Nieuwoudtville (AC), *Maguire 175* (BOL, NBG). 6 mi E of Nieuwoudtville, *Nordenstam 772* (NBG). Willems R., *Leipoldt 786* (SAM). Nieuwoudtville, *L. Bolus s.n.* (BOL-21067). Oorlogskloof-Nieuwoudtville, *Leipoldt 3851* (BOL). Calvinia-Nieuwoudtville (BC), *Goldblatt 3893* (MO); *Theron 1261* (PRE); *Mauve 4151* (M, PRE). 1 km W of Calvinia (BD), *Nordenstam & Lundgren 1069* (MO). Moordenaarspoort 26 mi N of Calvinia, *Lewis 2559* (SAM). 30 mi N of Calvinia, *Lewis 266* (SAM).

31.20 (Williston): Williston (BD), *Bayliss BRI 555* (K, M, MO, P, PRE, WAG). Calvinia-Williston, *Mauve 4152* (K, PRE). Near Williston, *Bayliss 6099* (MO), *Van der Schijff 7045* (J, PRE). Calvinia road N of Middelpos (C), *Barker 10769* (NBG).

32.18 (Clanwilliam): Near Clanwilliam (BB), *L. Bolus s.n.* (BOL); *Lewis s.n.* (BOL). Pakhuis Pass, *Compton et al. s.n.* (NBG-59117), *Barker 1998* (NBG); *Mauve 4657* (K, PRE). Kransvlei Mts., W of Clanwilliam, *Lewis 1857* (SAM). Algeria road near Clanwilliam Dam, *Goldblatt 2563* (M, MO, PRE, WAG). Old Clanwilliam road near Rondegat (BD), *Goldblatt 255* (BOL). Hillside near main road, S of Alpha, *Goldblatt 3928* (MO, WAG). The Rest (DB), *Salter 3605* (K). Pikeniers Pass-Porterville (DD), *Goldblatt 3920* (MO). Piketberg distr., *Taylor 3907* (NBG, PRE).

32.19 (Wuppertal): Welbedacht (AA), *Compton 6612* (NBG). Top of Pakhuis Pass, *Goldblatt s.n.* (MO). Bidouw valley, *Van Jaarsveld 1326* (NBG); *Marsh 401* (K, PRE, STE). Matjesrivier, Cedarberg (AD), *Wegener 150* (NBG).

33.18 (Cape Town): Langebaan (AA), *Salter s.n.* (BOL-31584). Mamre Hills (AD), *Barker 1763* (BOL, NBG). Between Darling and Mamre, *Johnson 176* (NBG). Near Moorreesburg (BA), *L. Bolus s.n.* (BOL-19145); *Weintraub s.n.* (J-19792). 20 km NW of Malmesbury on Hopefield road (BB), *Goldblatt 4082* (MO). Malmesbury (BC), *Lewis s.n.* (NBG-59118). Cape Town (CD), *Pappe s.n.* (SAM-70678, -70679, -70681). W slopes of Table Mt., *Lewis 680* (SAM). Signal Hill, *Phillips 719* (PRE, SAM); *Goldblatt 225* (BOL); *Page s.n.* (BOL-16189). Lions Head, *Zeyher 5018* (SAM). Road to Blaauwberg beach, *Barker 29* (BOL, K). Jonkershoek valley (DD), *Lewis 1656* (NBG, SAM). Lyndoch Station, *Goldblatt 4415* (MO). Stellenbosch flats, *Garside 262* (K).

33.19 (Worcester): Tulbagh (AC), *Hutchinson 361* (K). Hex River Valley (DA), *Wolley Dod 4024* (BOL, K).

33.20 (Montagu): Matjesfontein (BA), *H. Bolus s.n.* (BOL-14398); *Foley 13* (PRE). Whitehill karoo, *Compton 17418* (NBG). 2 mi S of Laingsburg (BB); *Vahrmeijer 2319* (PRE).

33.23 (Willowmore): W of Joubertina (DD), *Goldblatt 4946* (MO, NBG).

34.18 (Simonstown): Bergvliet farm (AB), *Purcell s.n.* (SAM-93377).

34.19 (Caledon): Caledon (AB), *Rogers s.n.* (SAM-48969). Caledon-Warm Baths Hotel, *Gillett 1076* (BOL, STE).

34.20 (Bredasdorp): Hassaquaskloof, near Stormsvlei (AA), *Ecklon & Zeyher 4075* (PRE, S).

34.21 (Riversdale): Hills near Riversdale (AB), *Muir 2679* (BOL, SAM).

Without precise locality: Richtersveld, *Marloth 6764* (BOL). Between Sutherland and Middelpos, *Hutchinson 719* (BOL, K, PRE).

Unknown locality: Layton, Fraserburg, *Shearing 53A* (K, M, PRE, S). Gounakraal, Fraserburg, *Wall s.n.* (S).

24. **Homeria pendula** Goldbl., sp. nov. TYPE: South Africa, Cape, Kamiesberg, *Goldblatt 4306* (MO, holotype; K, NBG, PRE, S, US, WAG, isotypes).—FIG. 27.

Plantae grandes, 50–75 cm altae, multiramosae. Cormus ca. 2 cm in diametro. Folia 3–4, ad 20 mm lata, caulis excedentia. Caulis erecta, ramis strictus, flexis subspathis. Spathae 4–5 cm longae, exterior parum brevior. Flores lutei, secundi vel penduli, tepalis reflexis; tepala exteriora 24–28 mm longa, ungue ca. 4 mm, erecto; interior parum parviora. Filamenta connata, columna ca. 15 mm longa; bulbosa ad basem; antherae 4–6 mm longae. Ovarium ad 10 mm longum; rami styli 2.5–3.5 mm longi, furcati ad apicem; sine cristis.

Plants tall, 50–75 cm high, much branched. *Corms* ca. 2 cm in diameter with black, coarsely reticulate tunics. *Leaves* 3–4, the lowermost basal, the others cauline, canaliculate, to 60 cm long, bent and trailing, to 2 cm wide. *Stem* straight, the branches erect, flexed below the spathes, the stem bracts dry-herbaceous, brown toward the apices. *Spathes* green, becoming dry above, 4–5 cm long, the outer slightly shorter than the inner. *Flowers* yellow, speckled with dark green in the center, secund to pendulous, the tepals reflexed at maturity; *outer tepals* 24–28 mm long, the claw ca. 4 mm long, erect and held against the filament column, the limb reflexed, narrowly ovate to elliptical, 7–8 mm wide, acuminate; inner tepals similar but slightly smaller. *Filaments* united, the column ca. 15 mm long, swollen abruptly above the base, tapering from the widest part to the apex, puberulous in the lower half; *anthers* 3–6 mm long, erect, contiguous, collapsing somewhat after anthesis, the pollen red. *Ovary* to 10 mm long; *style* branching

FIGURE 27. Morphology and distribution of *Homeria pendula*. Habit ×0.3; flower and outer tepal ×1; ovary and stamens ×2.5.

at anther base; *branches* 2.5–3.5 mm long, bifurcate, the arms 1 mm long, terete, initially obscured by the anthers, later apparent, extending beyond the collapsed anthers; crests lacking. *Capsule* 15–18 mm long, ± cylindrical, or narrowed towards the base. *Chromosome number* $2n = 12$.

Flowering time: October–early November.

Distribution: Kamiesberg, wetter places such as stream banks, seeps, etc.; above 1100 m; in sand; Fig. 27.

Surprisingly, although *Homeria pendula* is a common and conspicuous plant in the Kamiesberg, it has rarely been collected. It seems few botanists have collected here in October or later. It is one of the largest species of *Homeria*, and as it has many brightly colored and long-lasting flowers, it would be a most desirable horticultural subject.

Homeria pendula clearly seems to be closely related to the more widespread *H. miniata*, and both occur in the Kamiesberg, where *H. pendula* grows in wetter places than *H. miniata*.

SOUTH AFRICA. CAPE: 30.18 (Kamiesberg): Khamiesbergen (AC), *Leipoldt 3015* (BOL, K); *Leipoldt s.n.* (NBG-59243 cult.). Leliefontein, *Rodin 1461* (BOL, K, MO, WAG). Plateau above Studers Pass, *Goldblatt 4306* (K, MO, NBG, PRE, S, US, WAG). Streamsides near Welkom, E slopes of Rooiberg, *Goldblatt 4309* (MO, WAG). Leliefontein, foot of Eselskop, *Drège 8313* (S).

25. Homeria spiralis L. Bolus, J. Bot. 69: 260. 1931. TYPE: South Africa, Cape, Nieuwoudtville waterfall, *L. Bolus s.n.* (BOL-19348, lectotype; GRA, K, PRE, isolectotypes).—FIG. 28.

Plants small, 10–20 cm high, branched. *Corms* ca. 1 cm in diameter, the tunics black, coarsely reticulate. *Leaves* 3, the lowermost basal, the others cauline, linear, channeled below, flat above and loosely spiralled in the upper part, 2–4 mm wide. *Stem* flexuose, minutely papillate, the stem bracts 3–4 cm long. *Spathes* 2.5–5(–6) cm long, the outer about half the inner. *Flowers* salmon pink with yellow nectar guides and claws, the tepal bases forming a shallow cup narrowly windowed between the base of each, the limb outspread; *outer tepals* 16–23 mm long with a short ascending claw ca. 3 mm long, densely pubescent 1 mm above the base, the limb ca. 9 mm wide, narrowly ovoid or oblong; inner tepals smaller, 5–6 mm wide, obovate. *Filaments* united, the column 6 mm long, swollen above the base and then gradually tapering to the apex, densely pubescent in the bulbous part; *anthers* erect, contiguous, ca. 2 mm long, collapsing after anthesis to ca. 1.3 mm. *Ovary* 6–7 mm long; *style* dividing just above the anther base; *branches* short, deeply forked, hidden by the anthers, the arms slender, stigmatic at the apex, emerging between the anthers; crests absent. *Capsule* 10–13 mm long, ± cylindrical. *Chromosome number* $2n = 12$.

Flowering time: August to about mid September.

Distribution: Bokkeveld escarpment from Nieuwoudtville north and northwest; clay soils in renosterbosveld; Fig. 28.

Homeria spiralis is closely related to *H. miniata* and the two species have very similar flowers. They are, however, easy to distinguish from vegetative morphology; *H. spiralis* has a strongly flexuose stem, and narrow leaves that are loosely coiled distally. *Homeria miniata*, in contrast, has straight leaves and a more or less erect stem. *Homeria spiralis* has a restricted distribution, occurring along the northern edge of the Nieuwoudtville (Bokkeveld Mountain) escarpment, north of Nieuwoudtville.

SOUTH AFRICA. CAPE: 31.19 (Calvinia): Clay slopes near Nieuwoudtville waterfall (AC), *Goldblatt 3934* (MO, PRE WAG), *4336* (MO); *L. Bolus s.n.* (BOL-19348, GRA, K, PRE). Near Nieuwoudtville on Loeriesfontein road, *Lewis 5849* (NBG, STE). 18 km NW of Nieuwoudtville on Theunisdrift road (AA), *Goldblatt 3961* (MO, PRE, US, WAG).

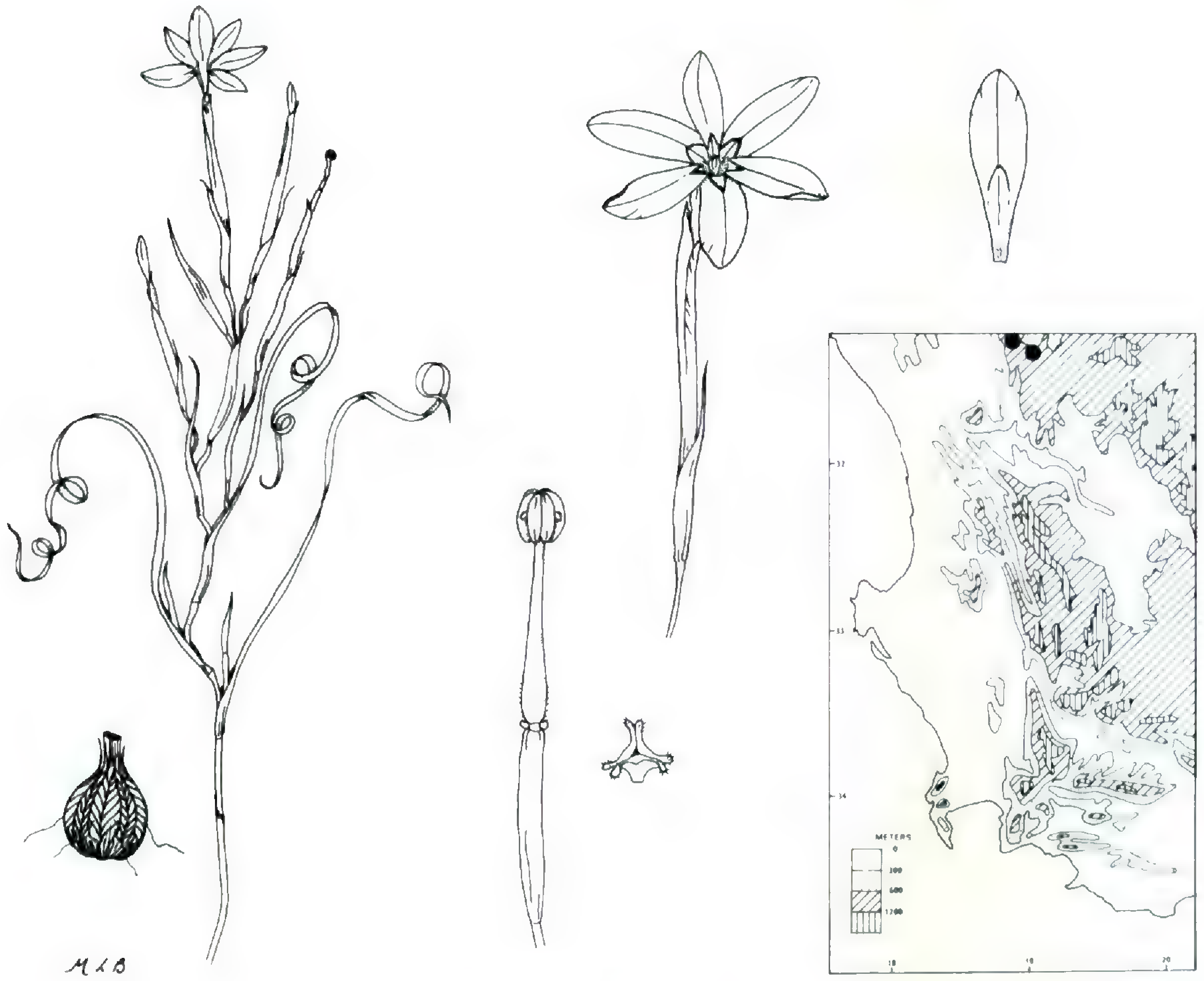

FIGURE 28. Morphology and distribution of *Homeria spiralis*. Habit ×0.5; corm, flower and outer tepal ×1; ovary, stamens and style branches ×3, the separated style branches ×6.

26. Homeria fenestrata Goldbl., sp. nov. TYPE: South Africa, Cape, Tanqua basin, 60 km S of Calvinia, *Goldblatt 3906* (MO, holotype; BR, K, NBG, PRE, S, US, WAG, isotypes).—FIG. 29.

Plantae parvae, ad 15 cm altae, pauciramosae. Cormus ca. 1 cm in diametro. Folia 2–4, inferiora supra terram inserta, canaliculata, lineares-filiformia. Caulis flexuosa. Spathae 3–3.5 cm longae, exterior circa dimidium interioris. Flores rosei, luteo ad centrum, ungues tepalorum infra cupuliformia, fenestrata inter tepala; tepala exteriora 15–21 mm longa, ungue ca. 3 mm longo, 1 mm lato, limbo 6–9 mm lato, oblongo-obovato. Filamenta connata, columna cylindrica, 6 mm longa; antherae 3 mm longae. Ovarium ad 4 mm longa; rami styli ca. 1 mm longa, bifurcata ad apicem; cristae obscurae.

Plants small, up to 15 cm tall, branched. *Corms* ca. 1 cm in diameter, the tunics black, reticulate. *Leaves* 2–4, the lowermost inserted well above ground, longer than the stem, channeled, linear, the upper shorter. *Stem* flexuose, all nodes below the spathes with produced leaves not bracts. *Spathes* 3–3.5 cm long, the outer about half the inner. *Flower* pink with yellow nectar guides edged with dark pink, faintly scented, the tepals cupped below but windowed between the narrow bases, spreading distally; *outer tepals* 15–21 mm long, the claw ca. 3 mm, less than 1 mm wide, and minutely papillate in the middle, the limb 6–9 mm wide, oblong to narrowly obovate; inner tepals slightly smaller, the limb obovate. *Filaments* united, the column cylindrical, 6 mm long, minutely papillate in the lower half; *anthers* erect, contiguous, 3 mm long, collapsing to 2 mm after anthesis.

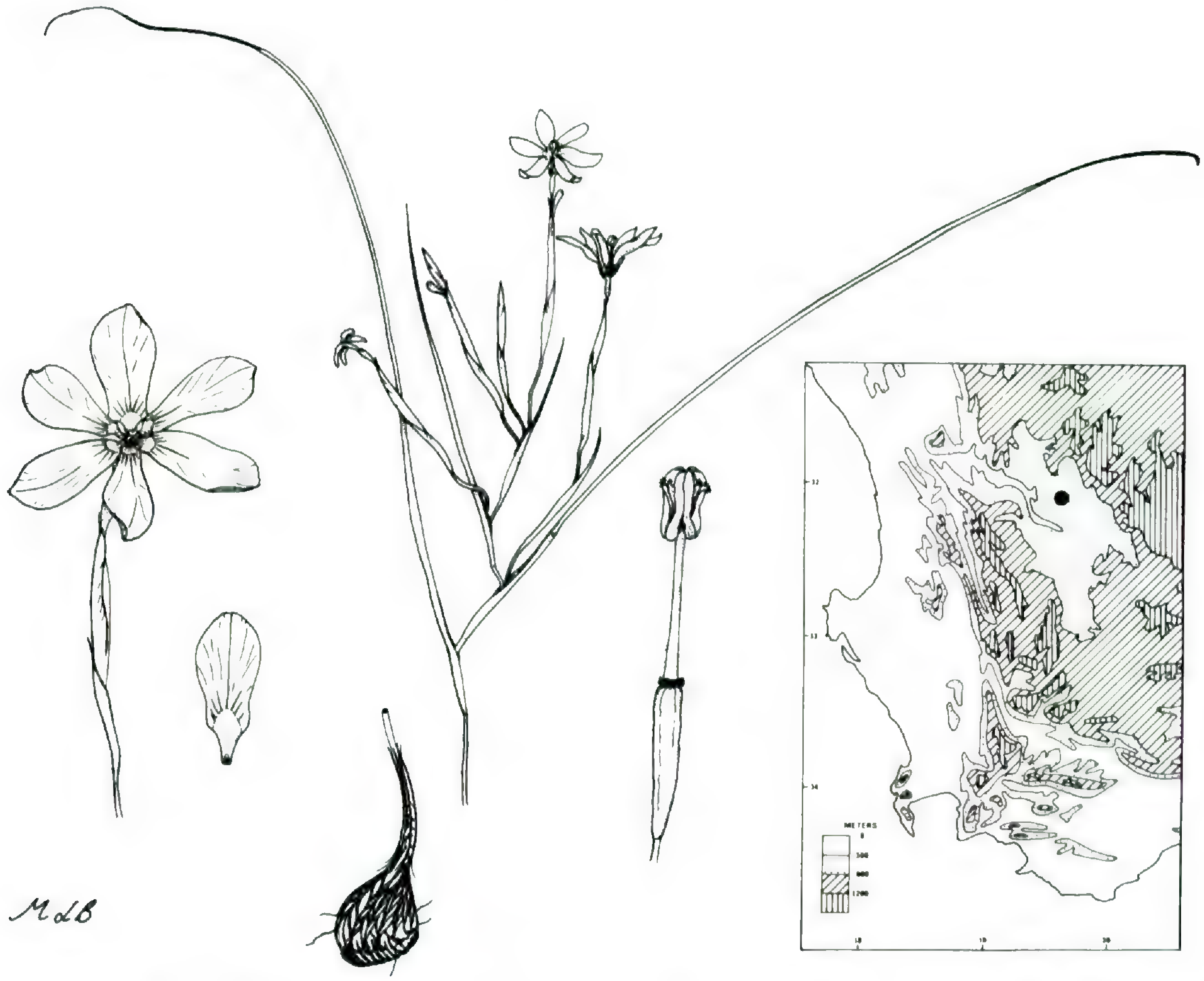

FIGURE 29. Morphology and distribution of *Homeria fenestrata*. Habit ×0.5; corm, flower and outer tepal ×1; ovary, stamens and style branches ×3.

Ovary ca. 4 mm long; *style* dividing near the anther base; *branches* 1 mm long, bifurcate, hidden by anthers, the arms stigmatic apically and emerging between the anthers; crests obscure, minute. *Capsule* and seeds not known. *Chromosome number* 2*n* = 12.

Flowering time: July–early August.

Distribution: Tanqua basin between the Cedarberg and Roggeveld escarpment; local on clay soil; Fig. 29.

Homeria fenestrata grows in the arid Tanqua-Doorn River basin between Calvinia and Ceres, where it is apparently fairly local. The species is known only from the type collection, made in August 1976, a particularly good spring for this area, which in many years receives virtually no rain and most species do not flower. It is closely related to *H. miniata* but can easily be distinguished by its slender filament column and narrowly clawed tepals.

SOUTH AFRICA. CAPE: 31.19 (Calvinia): 60 km S of Calvinia, Ceres road (DC), *Goldblatt 3906* (K, MO, NBG, PRE).

27. **Homeria tricolor** Lewis, S. African Gard. 23: 266. 1933. TYPE: South Africa Cape, Jan de Boers and Bonteberg Karoo, *Compton 3778* (BOL, lectotype; NBG, isolectotype). South Africa, Tunnel Siding, *Pillans s.n.* (BOL-14142, syntype); South Africa, Koo, cult. Whitehill Gardens, *Archer 686 sub Compton s.n.* (BOL, syntype).—FIG. 30.

Plants small to medium, 15–30 cm high, branched. *Corms* 1–1.5 cm in diameter, the tunics black, coarsely reticulate. *Leaf* solitary, basal, or rarely up to 3, with lowermost basal, linear, canaliculate, to 7 mm wide, exceeding the stem, distally often broken or trailing. *Stem* erect, usually flexed below each node, the bracts 3–6 cm long, the apices attenuate. *Spathes* 3.5–7 cm long, the outer about half as long as the inner, the inner elongating in fruit to enclose the ripening capsules. *Flowers* orange with a dark band near the tepal base, the center yellow, the tepals forming a wide cup 6–7 mm deep, 6 mm wide, the distal parts outspread; *outer tepals* 18–24 mm long, the claw 5–6 mm long, ascending, the limb horizontal, 7–8 mm wide, oblong to ovate; inner tepals slightly smaller, obovate. *Filaments* united, the column 7–9 mm long, slender, tapering slightly towards the apex, smooth or sparsely and minutely papillate; *anthers* erect, contiguous, to 3.5 mm long, collapsing to 2–2.5 mm after anthesis. *Ovary* 10–12 mm long; *style* branching near the anther base; *branches* short, 1.5–2 mm long, obscured by the anthers, bifurcate, the arms terete, emerging between the anthers; crests absent. *Capsule* 9–15 mm long, ± cylindrical, enclosed by the elongated inner spathe. *Chromosome number* $2n = 12$.

Flowering time: late September and October.

Distribution: from Barrydale and Laingsburg in the east to Koo and Karoopoort in the west; clay soils in dry renosterbosveld or karoo-scrub; Fig. 30.

Homeria tricolor is a fairly common, late-flowering species of the western Little Karoo and adjacent areas to the north between Laingsburg and Karoopoort. It is related to the more widespread *H. miniata* but differs not only in flower color and leaf number, but in the fundamental structure of the flower. *Homeria tricolor* has spreading tepals, which are cupped at the base, and a cylindrical filament column, while in *H. miniata* the short tepal claws are pressed against the base of the bulbous filament column. A closer relative is probably *H. fenestrata*, a rare species of the Tanqua basin to the north, which has a similar habit, but two or more leaves, while *H. tricolor* rarely has more than a single basal leaf. Two collections only are known of plants with more than one leaf, *Wall s.n.*, from Verlaten Kloof near Sutherland, and *Goldblatt 6302*, from the Koedoes Mts. These have up to three leaves, only the lowermost being basal.

SOUTH AFRICA. CAPE: 31.20 (Williston): Williston, koppie in town (BD), *Mauve 4131* (PRE).

32.20 (Sutherland): E of Bizansgat farm, Koedoes Mts. (CC), *Goldblatt 6302* (MO, NBG); Verlaten Kloof, Sutherland (DA), *Wall s.n.* (S).

33.19 (Worcester): Karoo Poort-Ceres (B), *Dymond s.n.* (BOL-21223). Tunnel Siding (BD), *Pillans s.n.* (BOL-14142). Top of Hex River Pass, *Goldblatt 3208* (MO, NBG). Koo (DB), *Archer 686* (BOL).

33.20 (Montagu): Jan de Boers and Bonteberg Karoo (AC), *Compton 3778* (BOL, NBG). Near

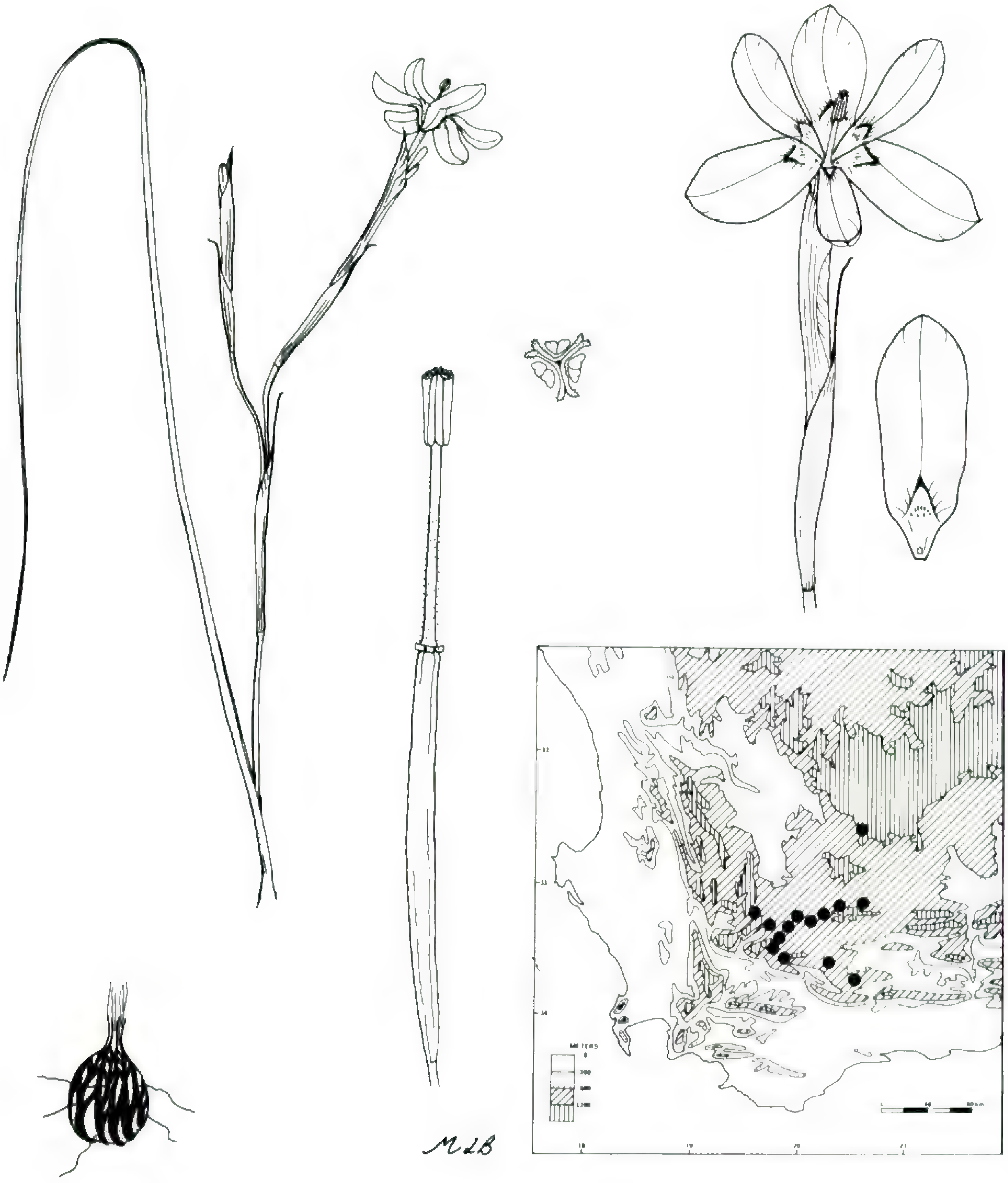

FIGURE 30. Morphology and distribution of *Homeria tricolor*. Habit ×0.5; corm, flower and outer tepal ×1; ovary, stamens and style branches ×3, the top view enlarged.

Matjesfontein and Dwars in de Weg (BA), *Marloth 9583* (B). Matjesfontein, *Fries et al. 1753* (LD, PRE, S); *Marloth 9586* (PRE). Whitehill Ridge, *Compton 15179* (NBG). Whitehill, Karoo Gardens, *Walgate 309* (NBG). Koppie N of Whitehill, *Thoday s.n.* (SAM-25203). Ouberg Pass, Touws R. distr. (CA), *Dymond s.n.* (BOL). 20 mi from Montagu on old Ladismith road (CB), *Lewis & Esterhuysen s.n.* (NBG-59222). Kalkoenhoek road, N of Montagu-Barrydale highway (CD), *Goldblatt 4183* (K, MO, NBG, PRE, WAG).

28. Homeria bifida L. Bolus, Ann. Bolus Herb. 3: 10. 1920. TYPE: Origin unknown, found growing at Kirstenbosch Botanic Gardens, *Page s.n.* (BOL-15815, holotype).—FIG. 31.

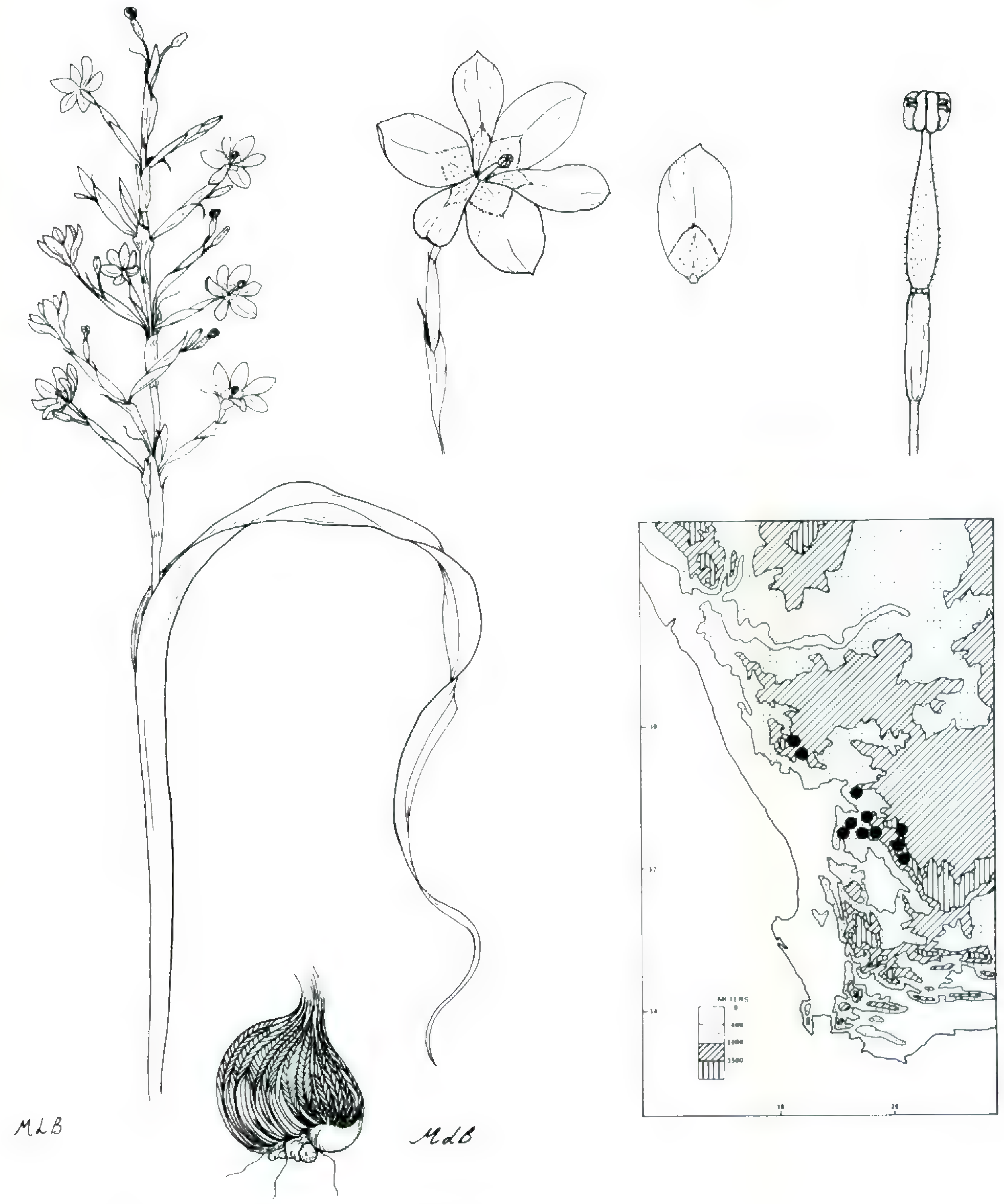

FIGURE 31. Morphology and distribution of *Homeria bifida*. Habit ×0.3; corm, flower and outer tepal ×1; ovary, stamens and style branches ×3.

Homeria salmonea L. Bolus, J. Bot. 69: 259. 1931. TYPE: South Africa, Cape, near Nieuwoudtville, *L. Bolus s.n.* (BOL-19542, lectotype; K, PRE isolectotypes).

Plants medium, to large, 20–75 cm tall. *Corm* 1.5–2 cm in diameter. *Leaf* solitary, basal, the lower part sheathing the stem, distally falcate, often broken and dry above, channeled, 15–20 mm wide. *Stem* erect, with a long basal internode, much branched from the upper nodes, the branches short, close to the

stem, flexed below the spathe, the spathes diverging from stem, the bracts 3–6 cm long. *Spathes* 3–4 cm long, the outer about two-thirds the inner. *Flowers* pale yellow or pink, the nectar guide deep yellow with green spots, the claw of the tepals short, ca. 2 mm, erect, appressed to the filament column, the limbs outspread; *outer tepals* 16–20 mm long, the claw narrow, 2 mm long, glabrous, the limb oblong to narrowly obovate, 9–14 mm wide; inner tepals slightly smaller, narrowly elliptical. *Filaments* united, the column 6–8 mm long, pubescent except at the very base and near the apex, abruptly swollen above the base, and then gradually tapering from the lower third to the apex; *anthers* ca. 2.5 mm long, shrinking to about 2 mm after anthesis, erect, contiguous. *Ovary* 7–9 mm long; *style* expanded above the filament column, dividing at the middle of the anthers; *branches* ca. 1 mm long, deeply forked, the arms stigmatic at tips, emerging between the anthers; *crests* lacking. *Capsule* ellipsoid, 10–12 mm long, 4 mm at the widest. *Chromosome number* $2n = 12, 12 + 4B, 24$.

Flowering time: August–September.

Distribution: mainly in the Calvinia district, but recorded to the north at Loeriesfontein and in the eastern Kamiesberg; mainly in clay soils; Fig. 31.

Homeria bifida was described from plants naturalized at the Botanic Gardens at Kirstenbosch and for many years the species was not matched with any known wild plant. I have examined the type material which includes good illustrations and am confident that *H. bifida* matches the northwestern Cape species known currently as *H. salmonea*. Since the latter was described much later than *H. bifida*, it must be reduced to synonymy. The species is closely related to the more wide ranging *H. miniata*, and the two are all but identical in flower structure. *Homeria bifida* can, however, be easily distinguished by its vegetative morphology, with its distinctive, broad leaf sheathing the lower part of the stem, and short crowded branching near the top of the stem. It is also closely related to *H. odorata*, a species restricted to the Nieuwoudtville area, which has a similar vegetative structure. Hybrids have been found in the wild between these two species. (See further discussion under *H. odorata*.)

SOUTH AFRICA. CAPE: 30.18 (Kamiesberg): Draaiklip (AA), *Pearson 6817* (K). 48 km E of Garies on Platbakkies road (AC), *Goldblatt 4053* (K, MO, NBG, PRE, WAG).

30.19 (Loeriesfontein): 7 km SW of Loeriesfontein (CD), *Goldblatt 3950* (BR, MO, NBG, PRE).

31.19 (Calvinia): Near Nieuwoudtville waterfall on Loeriesfontein road (AC), *L. Bolus s.n.* (BOL-19542, K, PRE). Nieuwoudtville waterfall, *Johnson 605* (NBG), *Lewis 2560* (SAM); *L. Bolus s.n.* (BOL-21004). Klipkoppies, 6 mi E of Nieuwoudtville, *L. Bolus s.n.* (BOL-19527). Glenlyon, Nieuwoudtville, *Goldblatt 3969* (C, MO, US); *Hardy 75* (K, PRE). 20 km W of Calvinia toward Loeriesfontein (BC), *Goldblatt 3942* (K, MO, WAG). Driefontein, voor Hantam (D), *Marloth 12819* (PRE). Slopes of Rebunieberg (DA), *Goldblatt 3894* (MO, K, NBG, PRE).

31.20 (Williston): 33 km SE of Calvinia, near Roggeveld escarpment (CC), *Goldblatt 4279* (MO, WAG).

32.19 (Wuppertal): Duiwelskop, Cedarsberg (?A), *Stokoe s.n.* (SAM).

29. Homeria odorata L. Bolus, Bull. Misc. Inform. 1932: 326. 1932. TYPE: South Africa, Cape, "Klipkoppies" near Nieuwoudtville, *L. Bolus s.n.* (BOL-19968, lectotype; K, isolectotype).—FIG. 32.

Plants medium 30–45 cm tall. *Corms* 1–2 cm in diameter, the tunics often softer in texture than usual and dark brown. *Leaf* solitary, basal, sheathing the lower part of the stem, falcate above, channeled, 12–20 mm wide. *Stem* erect, straight, with a long basal internode, much branched in the upper half, the branches short, held close to the stem, flexed below the spathe, the spathes diverging, the stem bracts 2–3 cm long, usually transparent and dry in the upper half. *Spathes* 3.5–4 cm long, the outer half to two-thirds the inner. *Flowers* pale yellow, rarely pale pink with a dark yellow nectar guide outlined in dull grey-green, sweet scented, the tepals forming a narrow cup in the lower part enclosing the filament column and anthers, spreading horizontally in the upper part; *outer tepals* 23–25 mm long, the claw ca. 8 mm long, erect, the limb oval, 9–11 mm wide; inner tepals slightly smaller. *Filaments* united, the column 4–5 mm long, wider at the base, tapering towards the apex, minutely puberulous in the lower half; *anthers* erect, contiguous, 1.5–2 mm long. *Ovary* 6–7 mm long, often speckled irregularly; *style* expanded above the filament column, dividing at the midline of the anthers; *branches* short, ca. 1 mm long, deeply forked, the arms ca. 0.5 mm long, stigmatic at the tips, emerging between the anthers or arching just above them; crests lacking. *Capsule* 7–10 mm long, to 5 mm wide, obovate-truncate. *Chromosome number* $2n = 12$.

Flowering time: mid August–September.
Distribution: very local round Nieuwoudtville; heavy red clay soil; Fig. 32.

Homeria odorata is known only from the area of Nieuwoudtville, in the Calvinia district, where it is fairly common in the heavy red clay soils found to the east of the town. It is closely related to *H. bifida* and their similarity in vegetative morphology is striking. The tepals of *H. odorata* are almost always pale yellow and form a narrow cup enclosing the stamens and style, the feature which distinguishes it from *H. bifida*. In the latter, which in the Nieuwoudtville area is usually pink, only the base of the filament column is enclosed by tepals, and the remainder of the column and stamens extend well beyond the tepals. The two species both occur around Nieuwoudtville, where *H. odorata* often seems to grow in the heaviest soils and *H. bifida* in rockier sites. At places where these habitats are adjacent, hybrids between the two species occur. The hybrids have been found to be completely sterile when grown in the greenhouse.

Specimens of an early collection, *Schlechter 10942* of this species bear the manuscript name *H. latifolia* Schlechter. Evidently Schlechter considered the species distinct but for some reason did not ever publish a description.

South Africa. cape: 31.19 (Calvinia): Oorlogs Kloof, hills (AC), *Schlechter 10942* (B, BOL, G, GRA, K, P, PH, PRE, S, US, Z). Between Nieuwoudtville and Oorlogskloof, *Leipoldt 3854* (BOL). Klipkoppies, 6 mi from Nieuwoudtville, *L. Bolus s.n.* (BOL-19968, GRA, K). Glenlyon farm, Nieuwoudtville distr., *Goldblatt 246* (BOL), *3967* (BR, MO, PRE, WAG).

30. Homeria fuscomontana Goldbl. sp. nov. type: South Africa, Cape, suurvlakte, N Cold Bokkeveld, plateau above Winkelhaaks R., *Esterhuysen 33951* (BOL, holotype; K, MO, PRE, S, isotypes).

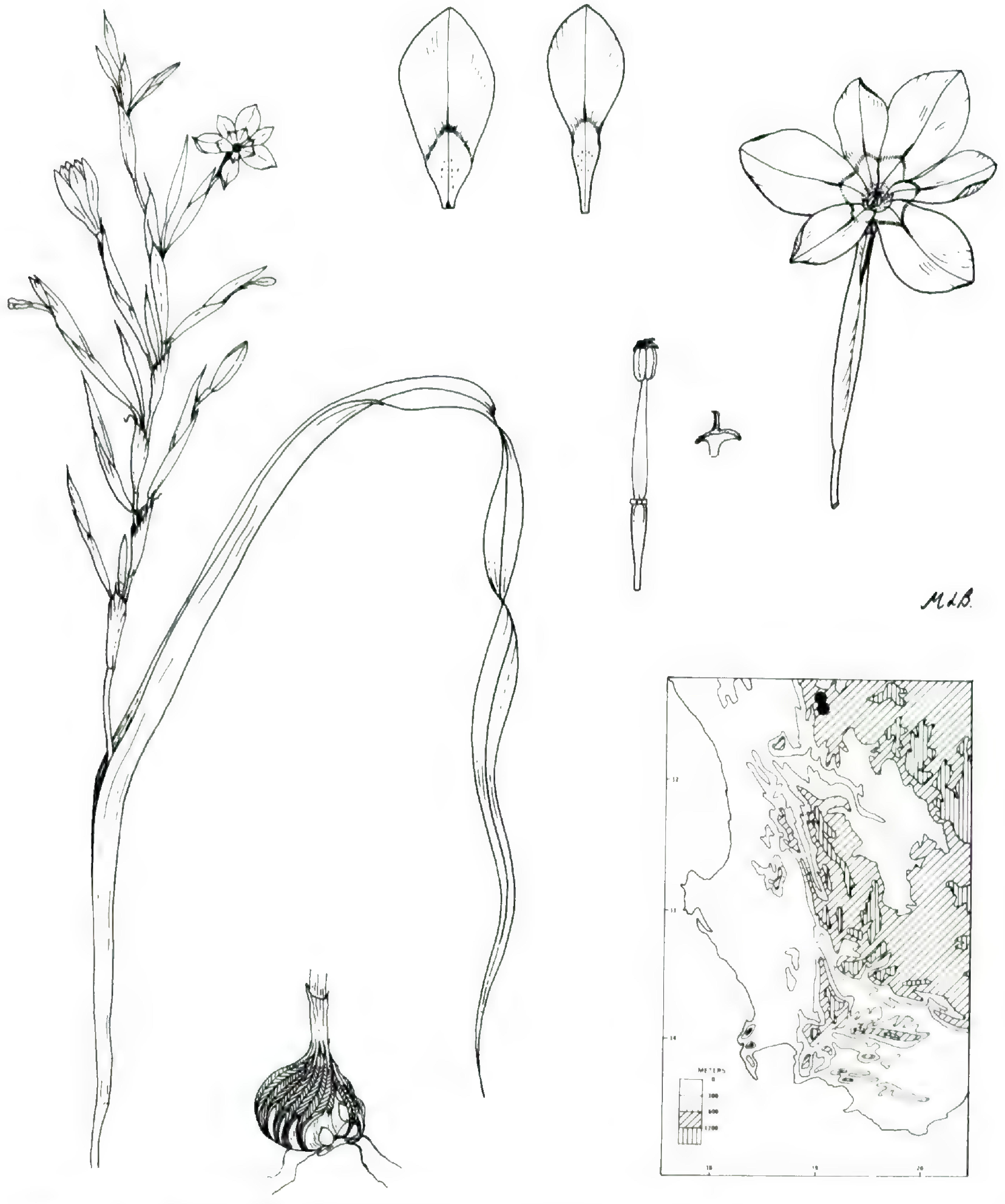

FIGURE 32. Morphology and distribution of *Homeria odorata*. Habit ×0.5; corm, flower, inner and outer tepal ×1; ovary, stamens and style branches ×3, the separated style branches enlarged.

Planta 10–25 cm alta. Cormus ad 10 mm in diametro. Folium unicum supra terram insertum, caulem excedens. Caulis flexuosus, aliquot ramosus. Spathae 2.5–4 cm longae, interior circa dupla longior exteriore. Flores flavi, ungues tepalorum cupulati circa basem filamentorum; tepala exteriora ad 22 mm longa, limbis 19 mm, interiora 20 mm longa. Filamenta connata, 6 mm longa, cylindrica; antherae 2–3 mm longae, connata. Ovarium 4–5 mm longum, inclusum, stylus divisus in medio antherarum, rami breves, 1.5 mm longi, bilobi.

Plant 10–25 cm high. *Corm* to 10 mm in diameter, tunics of dark fibers. *Cataphyll* solitary, dry, extending above ground, and becoming fibrous above. *Leaf*

solitary, inserted well above ground level, channeled, long and trailing. *Stem* erect below, flexed above sheathing base of leaf, bearing 1–several branches; stem bracts herbaceous, 2–3 cm long. *Spathes* 2.5–4 cm long, inner initially about twice as long as outer, but lengthening during flowering. *Flower* pale yellow, with deep yellow nectar guides towards base of tepal limb, with scattered green dots, tepal claws erect, forming a tube round lower half of filament column, limbs extending more or less horizontally; *outer tepals* oblong, obtuse, to 2.2 cm long, 8 mm wide, claw 3 mm; inner tepals ca. 20 mm long, narrow cuneiform, widest in upper third, to 7 mm wide. *Filaments* united, column 6 mm long, cylindric and pubescent in lower ⅔, tapering and smooth above; *anthers* initially ca. 3 mm long, erect, contiguous, collapsing after anthesis and less than 2 mm. Ovary 4–5 mm long, enclosed in spathes, style dividing at mid-anther level, branches short, ca. 1.5 mm, flat, bilobed, with arms curved outwards, protruding either side of subtending anther, stigmatic and ciliate at tips only. *Capsule* ovoid, to 8 mm long. *Chromosome number* 2n = 12.

Flowering time: September, flowers open between 10 and 11 A.M., close in the evenings and fade mid-morning two days later.

Distribution: stony slopes in the eastern Cold Bokkeveld, in arid fynbos; Fig. 33.

Homeria fuscomontana is a poorly known species, apparently related to the *H. miniata* complex. It has the stamens and style branches characteristic of section *Conanthera,* and the flowers resemble closely those of *H. miniata,* except that the filament column is cylindric rather than bulbous below, as is characteristic of *H. miniata.* It is readily distinguished from other species in the section by its single leaf inserted above ground level, the stem flexed above the leaf sheath and the small inflorescence spathes enclosing the ovary during development. *H. fuscomontana* is similar in vegetative characteristics only to *H. brachygyne* within the section but the latter has a larger, and papillate filament column (to 8 mm long) held well above the tepals, and salmon colored flowers. *H. fuscomontana* is diploid as are all the other species of section *Conanthera.*

The species is easily confused with *Homeria tenuis* and *H. flavescens* as these three species are similar in size and general appearance. Properly pressed or live flowers are needed for accurate determination.

SOUTH AFRICA. CAPE: 32.19 (Wuppertal) suurvlakte, N Cold Bokkeveld on stony plateau above Winkelhaaks R. (CD), *Esterhuysen 33951* (BOL, K, MO, PRE, WAG); Swartruggens, road to Katbakkies Pass, near Liberty, *Goldblatt 4188* (MO), *5344* (MO).

31. Homeria brachygyne Schltr., Bot. Jahrb. Syst. 27: 94. 1900. TYPE: South Africa, Cape, Bullshoek, Olifants R. valley, *Schlechter 8381* (B, lectotype; BOL, G, GRA, K, PRE, Z, isolectotypes).—FIG. 33.

Homeria papillosa L. Bolus, J. Bot. 69: 260. 1931. TYPE: South Africa, Cape, Van Rhyns Pass, *L. Bolus s.n.* (BOL-19541, holotype; K, PRE, SAM, isotypes).

Plants small to medium, 8–25 cm high, branched. *Corms* up to 10 mm in diameter, the tunics black, coarsely reticulate. *Leaf* solitary, inserted well above

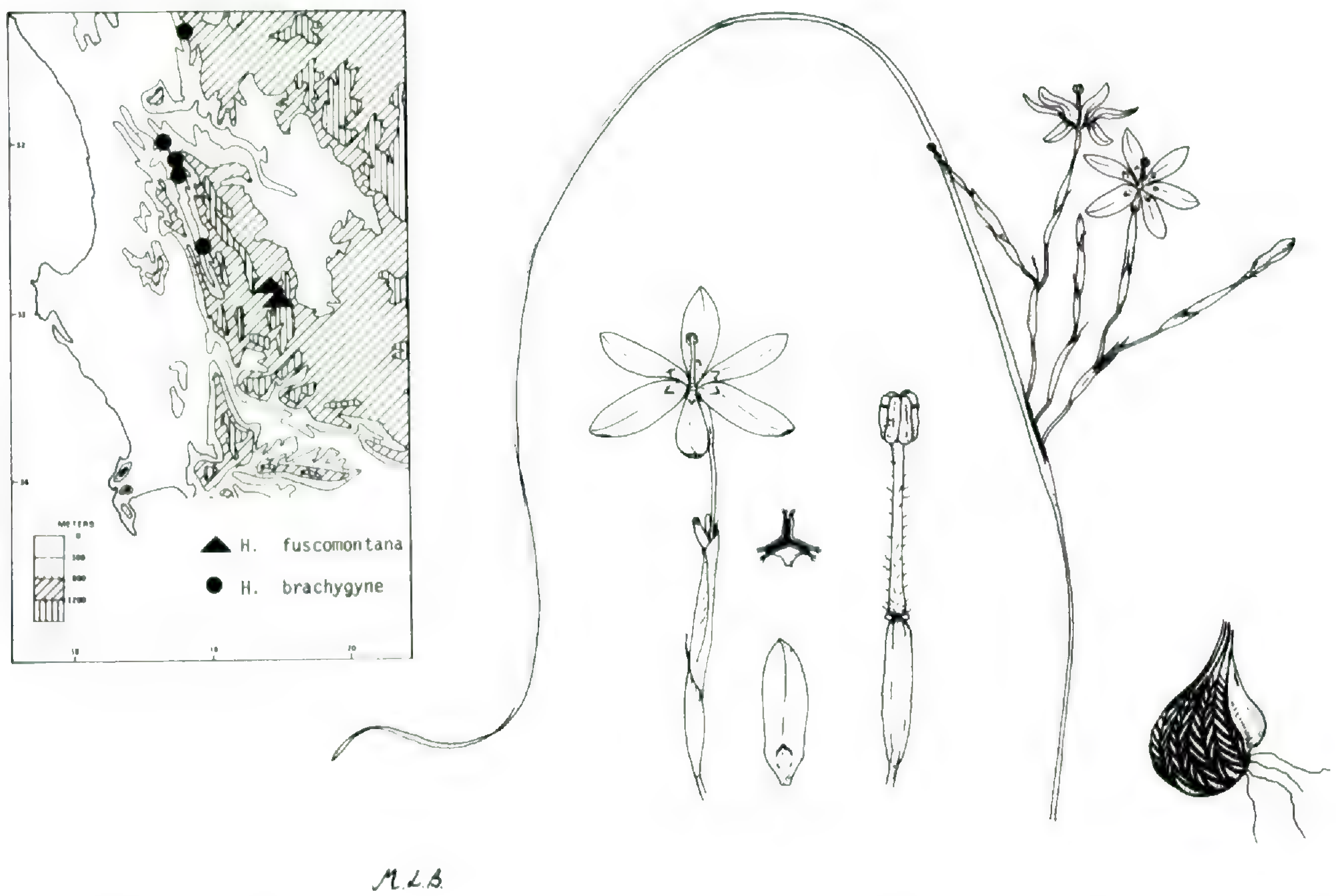

FIGURE 33. Distribution of *Homeria fuscomontana* and *H. brachygyne*, with morphology of *H. brachygyne*. Habit ×0.5; corm, flower and outer tepal ×1; ovary, stamens and style branches ×3, the separated style branches enlarged.

ground, linear, canaliculate to flat, 2–4 mm wide, longer than the stem; the lowermost stem bract sometimes with a free apex and ± leaflike. *Stem* flexed above the leaf insertion and above each stem bract, often densely branched, the bracts 1.5–2(–3) cm long. *Spathes* 3–5 cm long, the outer about half as long as the inner. *Flowers* salmon pink, the nectar guides yellow, the lower part of the tepals forming a shallow cup, the upper part outspread; *outer tepals* slightly larger than the inner, 18–22 mm long, the claw ca. 4 mm long, narrow, papillate towards the base, the limb obovate, often slightly pandurate, 6–9 mm at the widest point; inner tepals 5–6 mm wide. *Filaments* united, the column cylindrical, 6–8 mm long, papillate in the lower half; *anthers* to 3 mm long, erect, contiguous, collapsing after anthesis and seldom over 2 mm long. *Ovary* 5–6 mm long; *style* branching at the anther base; *branches* concealed by the anthers, short, bifurcate, the arms terete, stigmatic at the tips, the apices of the style branches emerging between the anthers; crests lacking. *Capsule* 8–10 mm long, ellipsoid; seeds many, angular. *Chromosome number* $2n = 12$.

Flowering time: late July–early September.

Distribution: Olifants River valley between Citrusdal and Klawer, and local to the north on Van Rhyns Pass; mainly on sandy soils; Fig. 33.

Homeria brachygyne is better known by its synonym, *H. papillosa*, a much later name, but comparison of the type material of *H. brachygyne* leaves no doubt

that the two species are identical. It is related to the widespread west coast and western Karoo species, *H. miniata*, and the two can easily be confused if examined superficially, as the flowers, in both size and color, are similar. *Homeria brachygyne* always has a flexed stem with a single leaf and a cylindrical filament column, features which readily distinguish it from the multi-leafed *H. miniata*, which has a noticeably bulbous-based filament column. The two species share the same range and may grow fairly close to one another, but *H. brachygyne* is usually found in sandy situations, and *H. miniata* usually grows in clay soils.

SOUTH AFRICA. CAPE: 31.18 (Van Rhynsdorp): Olifants R. valley, near Trawal (DC), *Goldblatt 3930* (K, MO, NBG, PRE). 23 km N of Clanwilliam, *Goldblatt 3931* (MO). Bullshoek, sandy places (DD), *Schlechter 8381* (B, BOL, G, GRA, K, PRE, Z). Clanwilliam barrage, *Compton 11057* (NBG).

31.19 (Calvinia): Van Rhyns Pass (AC), *Bond 1155* (NBG). 1.5 mi below top of Van Rhyns Pass, *L. Bolus s.n.* (BOL-19541, K, PRE, SAM). Near top of Van Rhyns Pass, *Goldblatt 261* (BOL), *131* (J).

32.19 (Wuppertal): Citrusdal vlei (CA), *Barker 3603* (BOL, NBG).

Locality unknown: Lammkraal, *Schlechter 10844* (B, BOL, G, GRA, K, LD, MO, P, PRE, S, US, Z).

EXCLUDED SPECIES

Homeria aurantiaca (Zuccagni) Sweet, Hort. Brit. ed. 2: 498. 1830.

Sisyrinchium aurantiacum Zuccagni in Roemer, Coll. Bot., Cent. 1: 145. 1807.
Homeria collina var. *aurantiaca* (Zuccagni) Baker, Handb. Irid. 72. 1892. Fl. Cap. 6: 28. 1896.

The name *H. aurantiaca* has long been applied to *H. flaccida* Sweet but as explained in the text, the type of the basionym *Sisyrinchium aurantiacum* was probably destroyed when Zuccagni's insect damaged herbarium was discarded. The description alone is insufficient for identification of the species.

Homeria flexuosa (L.f.) Sweet—This is a species of *Hexaglottis* currently known as *H. lewisiae* Goldbl.

Homeria herrei L. Bolus—This is a later synonym of *Helixyra spiralis* N. E. Brown, 1929, now *Barnardiella spiralis* (N. E. Brown) Goldbl. (Goldblatt, 1976c).

Homeria lilacina L. Bolus—This has recently been shown to be a synonym of *Moraea polyanthos* Thunb. (Goldblatt, 1979b) and is presently regarded as a species of *Moraea* (Goldblatt, 1980a).

Homeria maximilianii Schltr.—This has recently been placed in a separate genus *Rheome* (Goldblatt, 1980a), as *R. maximiliani* (Schltr.) Goldbl.

Homeria porrifolia Sweet, Hort. Brit., ed. 2: 498. 1830, nom. nud. The species name was listed with a reference to Curtis' Botanical Magazine, without page or plate cited. It has not been identified.

Homeria rogersii L. Bolus—This is now regarded as a synonym of *Moraea crispa* Thunb. (Goldblatt, 1979b) and is currently assigned to *Moraea* (Goldblatt, 1980a).

Homeria simulans Baker—This was treated as a species of *Moraea* (Goldblatt, 1976a) in which it required the new name *M. elsiae* Goldbl.

Homeria speciosa L. Bolus—This has been transferred to *Moraea* (Goldblatt, 1980a) as *M. speciosa* (L. Bolus) Goldbl.

Homeria spicata (Ker) Sweet sensu Klatt, Linnaea 34: 626. 1866. is *Hexaglottis virgata* (Jacq.) Sweet.

Homeria umbellata (Thunb.) Lewis—This has been assigned to the new genus *Rheome* (Goldblatt, 1980a) as *R. umbellata* (Thunb.) Goldbl.

Homeria virgata (Jacq.) Sweet—This is *Hexaglottis virgata* (Jacq.) Sweet.

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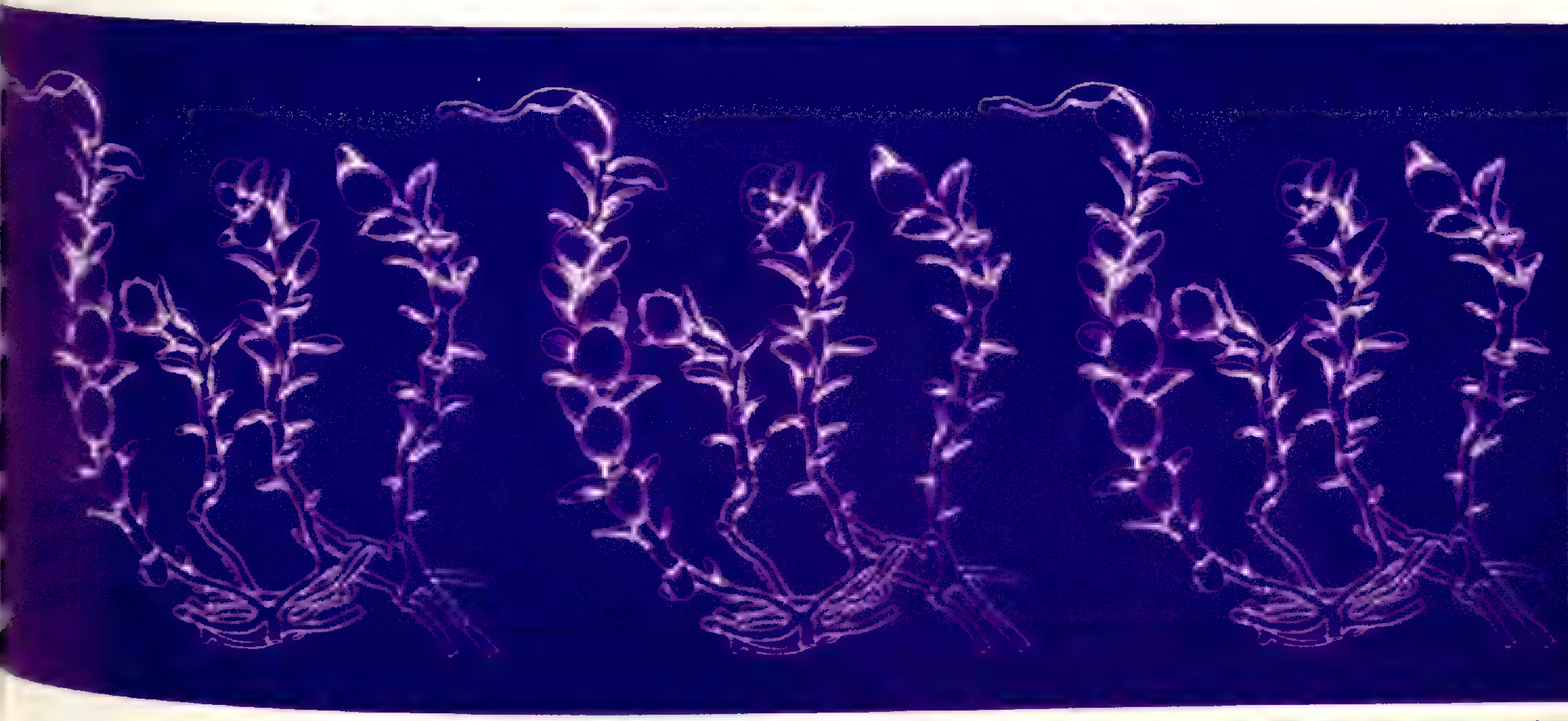

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NECTARIVORY AND POTENTIAL POLLINATION BY A NEOTROPICAL MARSUPIAL[1]

KIM E. STEINER[2]

ABSTRACT

The neotropical marsupial, *Caluromys derbianus*, the red woolly opossum, is a regular visitor and potential pollinator of *Mabea occidentalis* (Euphorbiaceae), an understory rainforest tree on Barro Colorado Island, Panama. *Caluromys* also visits and may pollinate nocturnal nectar-producing flowers of other plants. Nectar is an important food source for the red woolly opossum during seasonal lows in fruit abundance. Pollination by nonflying mammals may commonly occur in tropical forests in light of recent information on tropical tree distribution.

The importance of nonflying mammals including rodents, marsupials and primates as pollinators has become more widely accepted recently in light of an increasing number of more critical observations (Rourke & Wiens, 1977; Wiens & Rourke, 1978; Carpenter, 1978; Sussman & Raven, 1978; Lumer, 1980; Janson et al. 1981; Wiens et al., 1979; Hopper, 1980). With the exception of Lumer (1980) and Janson et al. (1981), these studies have focused on Old World systems, geographically limited to the Cape Region of South Africa, Madagascar, and Australia.

Australian marsupials have undergone extensive diversification as a result of radiation into a wide range of ecological niches that are filled by placental mammals elsewhere. This diversification includes forms such as the honey possum, *Tarsipes*, that regularly visit flowers (Hopper, 1980).

In the New World, marsupial radiation has been constrained by competition from placental mammals and has been confined to only two families, the Didelphidae and the Caenolestidae. Since little ecological information is available on

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the feeding habits of all but the common opossum, *Didelphis*, it is not surprising that floral visitation and pollination have been considered nonexistent for New World marsupials (L. G. Marshall, in Sussman & Raven, 1978). Although *Didelphis virginiana* has been reported visiting the flowers of *Ceiba pentandra* in Mexico (Toledo, 1977) and *D. marsupialis* in Panama (W. Glanz, pers. comm.), these reports, based on very limited observations in conjunction with other studies, provide little insight into the importance of flower visitation for these opossum species.

Caluromys derbianus, the red woolly opossum, is a relatively small (ca. 307 g), nocturnally active New World marsupial. It has a reddish and cream-colored body (180–290 mm) with a long (270–490 mm) prehensile tail. It is one of three species of woolly opossum and ranges from southern Mexico to Colombia and Ecuador (Walker, 1975). The other two species, *C. lanatus* and *C. philander*, are restricted to South America (Walker, 1975).

No information regarding the importance of various food types is available from field observations and even feeding experiments with captive *C. derbianus* are rare. *Caluromys*, according to Hunsaker (1977), is basically frugivorous, while Walker (1975) reports that a captive individual of *C. derbianus* ate bananas, young mice, and insects, including cockroaches. W. Glanz (pers. comm.) performed feeding experiments with fruits from the native environment (Barro Colorado Island, Panama) on a single animal and found that it preferred soft fruits such as *Ficus insipida* (Moraceae), *Eugenia nesiotica* (Myrtaceae), and *Spondias mombin* (Anacardiaceae) over hard-skinned fruit such as *Ficus yoponensis* and *Lacmellia panamensis* (Apocynaceae). The opossum also showed a definite pouncing behavior when faced with grasshoppers, cicadas, and katydids, all of which it ate.

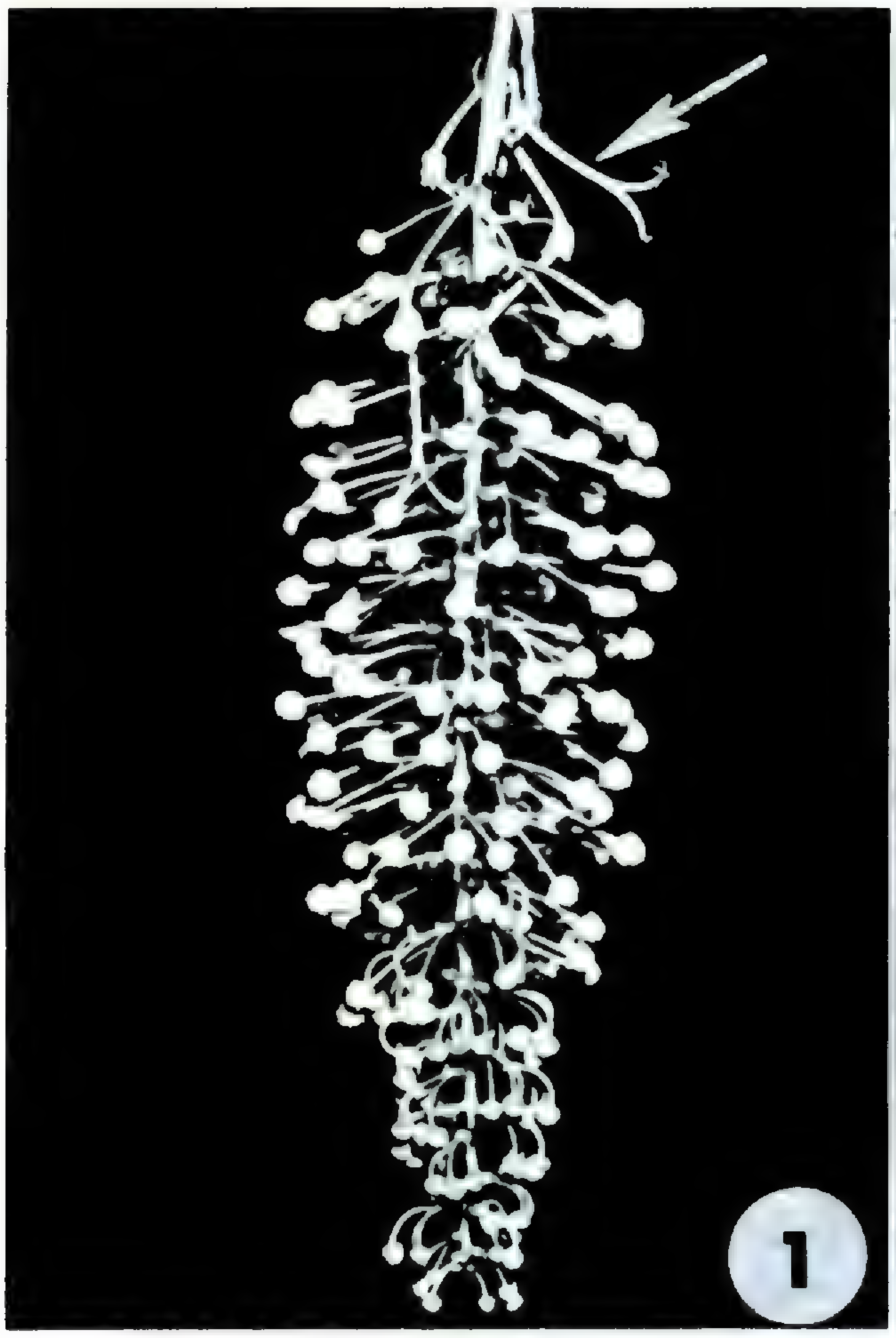
Nectar feeding by *C. derbianus* became apparent during a study of the reproductive biology of *Mabea occidentalis* (Euphorbiaceae) (Steiner, unpubl.). Observations at other nocturnally blooming flowers (*Ochroma pyramidale, Trichanthera gigantea*, and *Kigelia pinnata*), normally regarded as "bat flowers," reinforced the impression that *C. derbianus* commonly visits flowers for nectar.

As a result of initial observations, it was hypothesized that *Caluromys* acts as a pollinator of *M. occidentalis* and possibly other plants as well. To critically test this hypothesis, one should exclude all visitors except *C. derbianus* from the flowers and measure the resultant seed set. This was tried, but found to be unfeasible for *M. occidentalis* due to the difficulty of excluding bats and moths without excluding *Caluromys*.

Although selective exclusion experiments are unfeasible for *M. occidentalis*, I feel that the pollinating capability of *C. derbianus* can be assessed by addressing the following questions: 1. Is *Caluromys* a regular visitor? 2. Does *Caluromys* effectively transfer pollen from anthers to stigmas? 3. Is visitation synchronized with anthesis? 4. Does *Caluromys* visit the flowers nondestructively? 5. Is there interplant movement of *Caluromys*?

Study Site and Methods

This study was carried out over an 84-day period between 27 November 1979 and 19 February 1980 on Barro Colorado Island, located in Gatun Lake, a part



FIGURES 1, 3.—1. *Mabea occidentalis* at anthesis showing beads of nectar (× ca. ½). Arrow points to a pistillate flower.—3. *Caluromys derbianus* visiting an inflorescence of *Mabea occidentalis* (× ca. ¼).

of the Panama Canal (see Croat, 1978 for additional information on BCI). A total of 88.6 hours on 45 different nights was spent in observation. Observation time per night was quite variable, but averaged 1.9 hours (s.d. = 1.4).

During each period of observation, I recorded: (1) the time spent per inflorescence, (2) the number of inflorescences visited per tree, (3) the manner in which flowers were manipulated, and (4) the extent of interplant movement by the red woolly opossum. Observations were made using a headlamp equiped with a red plastic filter. Photographs were made with a 200 mm telephoto lens and a Vivitar 283 electronic flash. Live trapping of *Caluromys* was tried, but was unsuccessful.

Nectar volume and concentration were measured with calibrated micropipets and an Atago hand refractometer corrected to 23°C respectively. Glandular bracts on each inflorescence were marked and then bagged with nylon mosquito netting. The eight marked glandular bracts from five inflorescences on five different trees were sampled every hour from 1800 to 0500 EST or until nectar production ceased.

Mabea occidentalis, an understory tree of 4 to 6 m in height, flowers in Panama mainly in the dry season during the months of December through April (Croat, 1978). It ranges from Mexico to northern South America (Webster & Burch, 1968) and is particularly common on Barro Colorado Island.

Mabea occidentalis is monoecious with staminate and pistillate flowers clus-

tered in paniculate inflorescences that hang down from the tips of branches in the open areas between foliage layers. Each inflorescence is composed of about 200 staminate flowers and about 5 pistillate flowers. The staminate flowers are clustered in groups of three, subtended by a biglandular bract and borne on peduncles that are spirally arranged around a central axis (Fig. 1). Pistillate flowers are solitary and located at the basal nodes of the inflorescence. Although they usually hang down among the staminate flowers, little self-pollination occurs, since *M. occidentalis* is basically self-incompatible (Steiner, unpubl.).

RESULTS

FLORAL CHARACTERISTICS

The staminate flower clusters present pollen concomitantly with nectar secretion by the subtending biglandular bracts. An inflorescence secretes nectar for 2 or 3 nights with usually one-half to one-third of the staminate flowers reaching anthesis per night. Nectar secretion usually begins between 1630 and 1700 EST and can continue until 0700 the next day; however, at least 79% of the nectar is secreted before 2400. Nectar flow rate peaks for an average *Mabea* inflorescence between 1900 and 2200 and steadily declines thereafter. Nectar concentration starts at about 14% and eventually drops to about 9.5% g sucrose equivalents per 100 g of solution (Fig. 2). Each inflorescence produces a mean of 149 mg (s.d. = ±50 mg) sugar per night. The number of inflorescences secreting nectar per night for a given individual is quite variable, but is usually less than 20, except for unusually large trees.

VISITATION BEHAVIOR

The following observations were made to answer the questions posed in the introduction regarding the pollinating capability of the red woolly opossum: 1. *Caluromys derbianus* was a regular visitor to *Mabea occidentalis*. It was sighted on 30 of 45 observation nights. On 24 of the 30 nights, *Caluromys* was seen feeding at inflorescences, but because of intervening foliage, it was usually impossible to count the total number of inflorescences visited within a given tree. On one occasion, however, the opossum visited 27 inflorescences within a single tree. Although I never saw more than one individual at a tree, I twice saw two individuals in the same clump of trees.

2. The primarily arboreal red woolly opossum is very agile. Its strongly prehensile tail greatly enhances its manipulative capabilities as it often hangs down and holds inflorescences with its forepaws. This ability is necessary for successful foraging on *Mabea*, since the inflorescences hang down away from the foliage at the tips of small branches. Figure 3 shows *C. derbianus* removing nectar from a *Mabea* inflorescence; it does this by lapping up the nectar droplets that cling to the biglandular bracts. This process lasts an average of 13.5 seconds (s.d. = 5.4, n = 41) and results in complete removal of the nectar. While actively foraging within a tree, *Caluromys* visits a mean of 1.6 inflorescences per minute (s.d. = 0.5, observation periods, n = 8, of ≥7 minutes). As the red woolly opossum removes nectar, its snout contacts the staminate flowers (Fig. 3) and becomes covered with pollen. Although not apparent in black and white photographs such

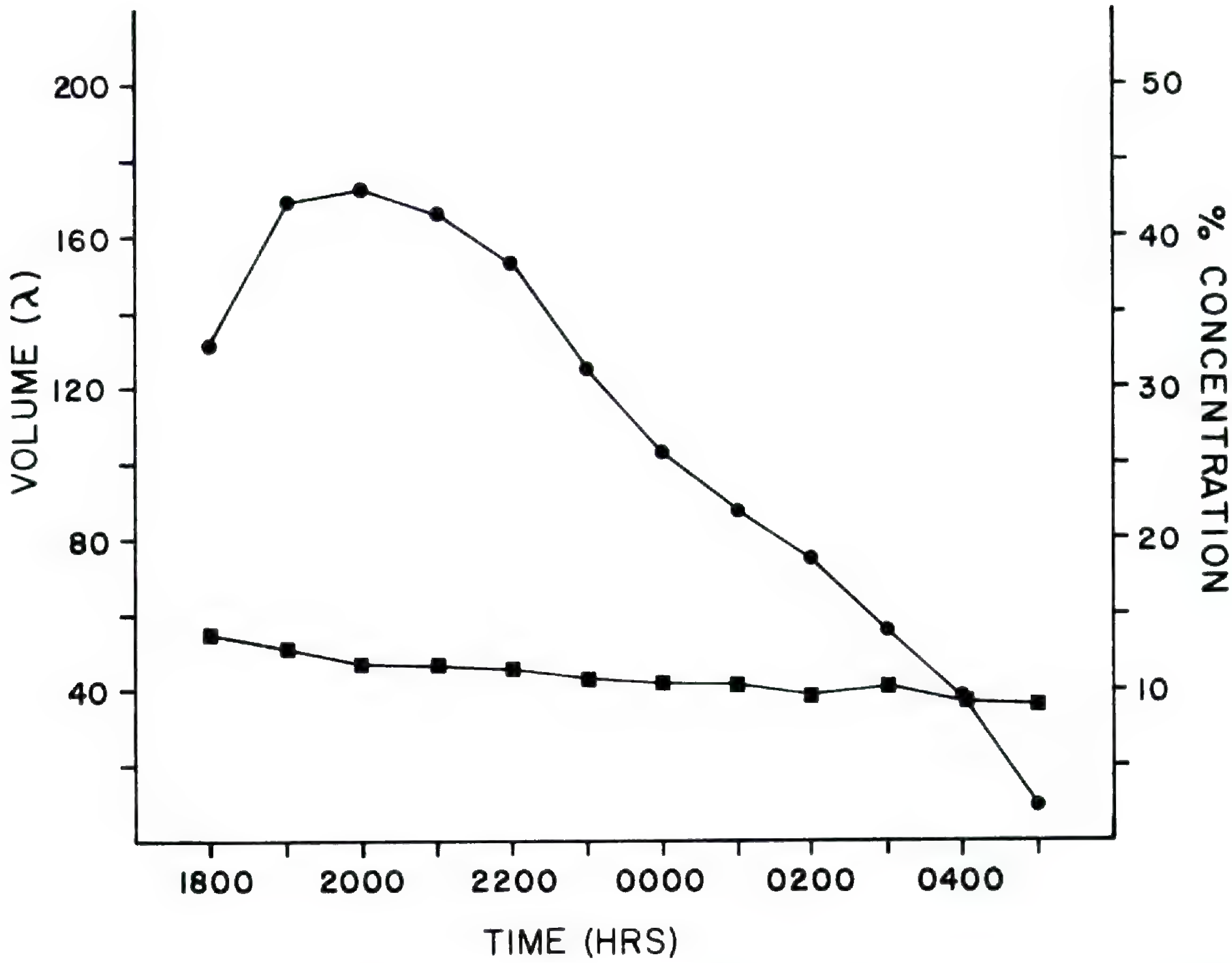


FIGURE 2. Mean nectar volume (λ) (solid dots) and concentration [(g sucrose equivalents per 100 g solution) %] (solid squares) vs. time. The means are based on the average nectar production of a single glandular bract × the average number of glandular bracts secreting nectar per inflorescence per night.

as Fig. 3, the presence of bright yellow pollen on the snout can be readily detected in color photographs. The pistillate flowers usually contact the opossum's snout as well (although not shown in Fig. 3), since they hang down among the staminate flowers. Although live traps were set out so that pollen loads could be collected and analyzed, no *Caluromys* were captured. Behavioral observations strongly suggest that effective pollen transfer occurs, but this cannot be conclusively shown without using marked pollen or some type of powdered dye.

3. Visitation by *C. derbianus* is well synchronized with anthesis. All observations of the opossum were between 1900 and 2400 EST, the period of maximum nectar secretion (Fig. 2), pollen presentation and stigma receptivity (Steiner, unpubl.).

4. I observed *Caluromys* visits to 215 inflorescences with no sign of damage to the flowers. Floral parts were not eaten nor were any broken off in handling. *Caluromys derbianus* visits *M. occidentalis* flowers primarily for nectar; however, it cannot help but ingest pollen at the same time. Additional pollen consumption was observed during grooming periods.

5. *Mabea occidentalis* generally occurs in discrete stands in the young (ca. 70 yr old) forest on BCI (DeSteven, in press; Steiner, unpubl.). Most of the red woolly opossum observations were made at one such stand. Although the trees

were closely spaced [mean nearest neighbor distance (trunk to trunk) = 2.45 ± 1.02 m, n = 12], it was often difficult to follow movement from one tree to another due to the presence of other vegetation. The canopies of most of these trees were overlapping and thus provided easy access for the arboreal woolly opossum. During the study period, 53 interplant movements were recorded. On January 9, *Caluromys* was followed for an hour, while it visited seven trees. Foliage obstructed my view, so that I could not count every inflorescence visited, but I did see at least one inflorescence visit in each tree. The foraging loop lasted one hour, however about 18% of this time was spent grooming, while the opossum remained stationary.

On BCI, *C. derbianus* was seen visiting flowers of two other species. This opossum fed at *Ochroma pyramidale* flowers on two of seven nights of which observations of one or more hours were made. The longest visit was on February 12 when *Caluromys* was present for an hour. During that time, it made a total of seven visits to three different flowers on two adjacent trees. Actual foraging time was only about 5 minutes, while the rest of the time was spent sitting and grooming. Two *Caluromys* individuals were present in these same trees for over 30 minutes on January 12 (M. Tuttle & L. Taft, pers. comm.).

Although I saw *Caluromys* on *Ochroma* only twice during the observation period, *Didelphis marsupialis* individuals were present the entire time on five of seven nights. On these nights, as many as three individuals were seen foraging within a single canopy. Although movement between overlapping canopies occurred, movement to more distant trees was uncommon.

Didelphis, although well suited to foraging on *Ochroma* with its sturdy flowers and branches, lacks the small size and agility which would permit it to exploit *M. occidentalis* as a nectar source. *Didelphis* was seen several times on the ground in the vicinity of *Mabea* and caught in traps on the sturdier branches around *Mabea* inflorescences, but it was never seen visiting the flowers.

Caluromys was seen twice visiting a heavily (ca. 100 flowers) flowering individual of *Trichanthera gigantea* (Acanthaceae) during a 5 day period from February 28 to March 3. The red tubular flowers of *Trichanthera* are clustered on leafless stalks that project up and out from the foliage. Both visits by *Caluromys* were brief. The longest visit lasted 9 minutes during which 8 flowers were visited. Heavy visitation by *Glossophaga soricina*, a small nectar-feeding bat and primary pollinator (Steiner, unpubl.), probably kept nectar levels too low for profitable foraging by *Caluromys* during these observations.

DISCUSSION

Since *Caluromys* appears to be capable of pollinating *Mabea occidentalis*, it is important to ask whether *M. occidentalis* shows adaptations which suggest coevolution between it and the opossum. The answer is no. The inflorescences of *Mabea*, although visited by noctuid and pyralid moths, cerambycid beetles, and *Trigona* bees, in addition to *C. derbianus*, are most clearly adapted to pollination by bats (Steiner, unpubl.). Nocturnal anthesis, exposed position outside the foliage, drab coloration, strong musty nocturnally produced odor, and production of relatively large amounts of pollen and nectar all characterize the inflorescences of *M. occidentalis* (Steiner, unpubl.), as well as the chiropterophi-

lous syndrome as presented by Faegri & van der Pijl (1979). Bats were commonly observed visiting *Mabea* inflorescences on BCI (Steiner, unpubl.).

Although *C. derbianus* appears capable of pollinating *M. occidentalis*, its importance as a pollinator is not clear. Observations (Steiner, unpubl.) suggest that *C. derbianus* may vary in importance as a pollinator over the flowering period of *M. occidentalis* depending on the corresponding bat visitation rate. However, only controlled selective exclusion experiments can resolve this question satisfactorily.

The importance of nectar in the diet of neotropical mammals may fluctuate seasonally. Animal-dispersed fruits are scarce at the end of the wet season and beginning of the dry season (November–February) on Barro Colorado Island (Smythe, 1970). It is at this time that most bat-pollinated species flower (cf. Croat, 1978), as they do in Costa Rica (Heithaus et al., 1975). It is not surprising, therefore, that bats and other animals exploit nectar during this period. In Costa Rica (Heithaus et al., 1975) and to a lesser extent on BCI (Bonaccorso, 1979), bats such as *Artibeus jamaicensis* and *A. lituratus* that are normally frugivorous during most of the year become common flower visitors during this season.

Is nectar an important energy source for *Caluromys*? One can calculate the energy requirement of a marsupial using the equation SMR = $48.6 \times W^{.75}$ kcal/day derived by Dawson & Hulbert (1970), where SMR is standard metabolic rate and W is the weight of the animal. Substituting in the average weight of *C. derbianus* [307 ± 72 g, n = 20 (based on specimen labels from Panamanian collections of *C. derbianus* in the National Museum, Washington, D.C.)], gives a SMR = 20.0 kcal/day. If one assumes an activity/feeding rate of 2 SMR, the daily energy requirement becomes 40.0 kcal. Since the sugar in nectar yields about 3.8 kcal/g, the red woolly opossum would require about 10.5 g of sugar/day. If its assimilation efficiency is 95% [Howell (1979) found a 96–99% assimilation efficiency for bats], then *C. derbianus* would have to ingest 11.1 g of sugar.

Mabea occidentalis produces an average of 149 mg sugar per inflorescence per day. To satisfy its daily requirement, therefore, *C. derbianus* would have to consume all of the nectar produced by 74 inflorescences. *Caluromys* concentrates its visits during the peak period of nectar secretion (i.e., 1900–2400 EST). Seventy-nine per cent of the total nectar produced is secreted before 2400 EST; therefore, if *C. derbianus* limits its visits to this time interval, it must visit 94 inflorescences.

Although no woolly opossums were marked, the visitation patterns observed at the main study site suggest that most visits were by a single individual. An individual *C. derbianus* was observed to either stay in the clump of flowering trees for several hours with inactive periods interspersed between foraging bouts or to make 2–3 foraging loops during an evening, but leave the clump after each loop for a variable amount of time. Unfortunately I was unable to follow the opossum once it left the study area. If to get all of the nectar produced by an inflorescence by 2400 EST a woolly opossum makes 3 visits to a given inflorescence, it would need to make 281 inflorescence visits in an evening.

While actively foraging, *C. derbianus* was found to visit 1.6 inflorescences per minute, therefore visits to 281 inflorescences would require about 176 minutes (2 hr 56 minutes) of foraging time, a little over half the time available between 1900 and 2400 EST.

It is not likely that 94 inflorescences were secreting nectar in the study area; however, if *C. derbianus* traplines between different clumps, which is suggested by its periodic departures, it could conceivably visit this many inflorescences. Even if *C. derbianus* visited only half this number of inflorescences, it would still be consuming a significant portion of its daily requirement. Since *C. derbianus* is omnivorous, there is no reason to assume that all of its calories must come from nectar. A diet consisting entirely of nectar would probably be nutritionally inadequate as it is for some rodents (D. Wiens, pers. comm.); however, ingestion of pollen along with nectar may help alleviate this problem as it does for some bats (Howell, 1974).

The following additional observations suggest that nectar is an important food source for *C. derbianus*. W. Glanz (pers. comm.) has seen red woolly opossums along with kinkajous (*Potus flavus*) in flowering trees of *Ceiba pentandra*. Steiner (pers. obs.) has seen *Caluromys* visiting a *Kigelia pinnata* (an Old World bat-pollinated tree) individual, while R. Zell (pers. comm.) observed *C. derbinaus* at a nectar feeder in Gamboa (former Panama Canal Zone). P. Charles-Dominique (pers. comm.) has observed another *Caluromys* species, *C. philander*, visiting large flowering trees of *Inga thibandiana*, *I. ingoides*, and *Hymenaea courbaril* in French Guiana.

Mabea occidentalis, *Ochroma pyramidale* (=*O. lagopus*) (Vogel, 1954), and *Trichanthera gigantea* (Vogel, 1969) have quite different floral morphologies, yet all three possess characteristics which adapt them to pollination by bats. On Barro Colorado Island, all of these species are indeed visited by bats (Steiner, unpubl.).

Flowers that utilize bats as pollen vectors usually provide relatively large amounts of food in the form of nectar. Associated with these flowers is a musty or fermented odor that acts as an important attractant. Since this odor signals a rich food supply, one would expect other nocturnal mammals to locate and utilize such food sources. It is, therefore, surprising that more nonflying mammals have not been reported visiting bat pollinated flowers in the New World tropics.

Until recently, tropical lowland forest trees have been considered to be uniformly dispersed and present as adults in low densities. Since most tropical trees are self-incompatible (Bawa, 1974), reproductive success is dependent on outcrossing. In such a system, long-distance pollinators (e.g., large bees, sphingid moths, bats, and hummingbirds) must play a disproportionately greater role in pollination than less mobile animals. However, since the foraging ranges of these less mobile animals are so poorly known, such a generalization must be made with caution. If all bat-pollinated trees are highly dispersed, it is unlikely that effective pollen transfer between conspecifics by a nonflying mammal such as *C. derbianus* would occur.

The classical notion of tropical forest tree distribution has been challenged by Hubbell (1979) as a result of work done at a tropical dry forest site in Costa Rica. He found that most trees were clumped rather than highly dispersed. In his study area, approximately 20% of the individuals of *Hymenaea courbaril*, a bat-pollinated tree, had touching canopies (S. P. Hubbell, pers. comm.). In a mass-flowering individual of this same species in French Guiana, P. Charles-Dominique (pers. comm.) saw 6–8 individuals of a related woolly opossum, *C. philander*,

visiting flowers. The fact that many neotropical trees such as *M. occidentalis* (Steiner, unpubl.), *Ochroma pyramidale* (pers. obs.), and *Hymenaea courbaril* (Hubbell, 1979) are clumped suggests that opportunistic nectar feeding by *Caluromys* or other nonflying mammals may often result in effective pollination in neotropical forests.

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A CONTRIBUTION TO THE FLORAL BIOLOGY AND REPRODUCTIVE SYSTEM OF *COUROUPITA GUIANENSIS* AUBL. (LECYTHIDACEAE)[1]

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Abstract

Studies of the reproductive system and pollination syndrome of cultivated trees of *Couroupita guianensis* Aubl. are presented. The first report of the internal morphology of the stigma is included. In the stigmatic area two parts can be distinguished, one is hydrophobic and is composed of conspicuous collector hairs and the other is hydrophilic and is formed by the top of the transmission tissue; both parts have important functions in fertilization. The flowers are odoriferous, nectarless and are visited by bees for their pollen. Osmophores are more evident in the top of the filaments of the hood anthers. The pollen is morphologically and physiologically dimorphic. The fertility of the pollen was tested, "in vivo" and "in vitro"; under both conditions, only the staminal ring pollen germinated. The species is self-compatible. Pollen tubes begin to develop in 45 minutes and arrive at the ovules in 24 hours. The field observations and tests demonstrate that the species studied, although allogamous, is self-compatible.

The Neotropical Lecythidaceae have been studied mainly with reference to the floral biology, focusing on the androecium.

Monteiro-Scanavacca (1975), basing her studies on the vascular system of Lecythidaceae species, concluded that in this family the application of the term androphore is erroneous, and defined the structure in question as a body of fused stamens.

Prance (1976) studied the pollination of six Amazonian species of Lecythidaceae from five genera, describing the complex androphore structure and the pollinators. Prance & Mori (1977) discussed androecium and fruit terminology of Lecythidaceae and commented on the similarity between the genera *Lecythis* and *Couroupita*. Mori et al. (1978) classified the New World Lecythidaceae in three basic types according to floral structures: those with actinomorphic androecium being the most primitive (e.g., *Gustavia*), those with zygomorphic hood, flat (e.g., *Couroupita*) and coiled (e.g., *Escheweilera*), being more advanced. Mori & Orchard (1979) described the dimorphic morphology and physiology of the pollen of *Lecythis pisonis* Camb. and compared this pollen with that of *Couroupita guianensis*.

The gynoecium, until now, has only been studied with reference to placentation. Monteiro-Scanavacca (1974), in her studies of 12 species of Lecythidaceae, concluded that the basal portion of the ovary is multilocular with axillary placentation, becoming unilocular with parietal placentation in the distal portion.

In this paper the floral biology and reproductive system are discussed and the stigmatic region, style, and the tissues involved in fertilization are defined. The

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pollination syndrome and the intrafloral behavior of pollinators are analyzed. We tested the species for autogamy, self-compatibility, and outbreeding. The strong fragrance released by the flower of this species induced us to also study the internal morphology of the osmophores.

Materials and Methods

The study material was obtained from 13 trees cultivated in the "Horto Botânico do Museu Nacional" of Rio de Janeiro (Brazil). To study the reproductive system the following tests were used:

Direct Autogamy (Font Quer, 1977).—120 flower buds were enclosed in pollination bags to check for the occurrence of autogamy; 20 of these were observed microscopically to verify pollen deposition on the stigmatic area, while the rest were left bagged.

Self-compatibility.—120 flower buds were enclosed in pollination bags and self-pollination was performed artificially (indirect autogamy); 20 of these flowers were pollinated with pollen from the hood and the remainder, with pollen from the ring. Pollen tube formation and development was observed in fresh sections of the stigma, style and ovary, at different times up to 24 hours after anthesis, for both ring and hood pollen.

Outbreeding.—50 flower buds were bagged and cross-pollinated. Pollen from the ring and the hood was tested with aceto carmine to show presence of significant amounts of protoplasm (Linsley & Cazier, 1963). Pollen tube development was studied in the same manner as described above. Fruit development was observed. The stigmatic area was studied in longitudinal and transverse fresh sections stained with Cotton Blue. The presence of lipids and sugars in stigmatic secretions was detected with Sudan III and Sudan IV and Fehling's reagent (Jensen, 1962). Fertility of hood and ring pollen was determined "in vitro" using the technique outlined by Mori & Orchard (1979). Osmophores were detected with Neutral Red (Vogel, 1963) and thorough studies were made of the internal morphology of different verticils of the floral bud, before and after anthesis.

Results, Discussion and Conclusion

Field Observations

The flower of *Couroupita guianensis* is large and strikingly showy with a zygomorphic androecium and a great number of stamens. The corolla has 6–8 petals, the adaxial petal face is purple and the abaxial face is yellow.

Floral patterns, in both visible and ultraviolet light, are very distinctive. Under UV light only the anthers of the hood reflect, presumably serving as pollinator guides. Distinctive floral patterns can serve as guides for a specific pollinator and can be regarded as a potentially important factor in maintaining the separation of sympatric species (Scogin et al., 1977; Jones & Buchmann, 1977). We consider floral patterns as an additional factor to be added to Mori et al.'s (1978) selection of characters that reduce competition for pollinators between different species of Lecythidaceae.

The flowers are odoriferous, nectarless, and are visited by bees for their pollen. Pollen from anthers of the hood constitute a rich source of nutrition for the

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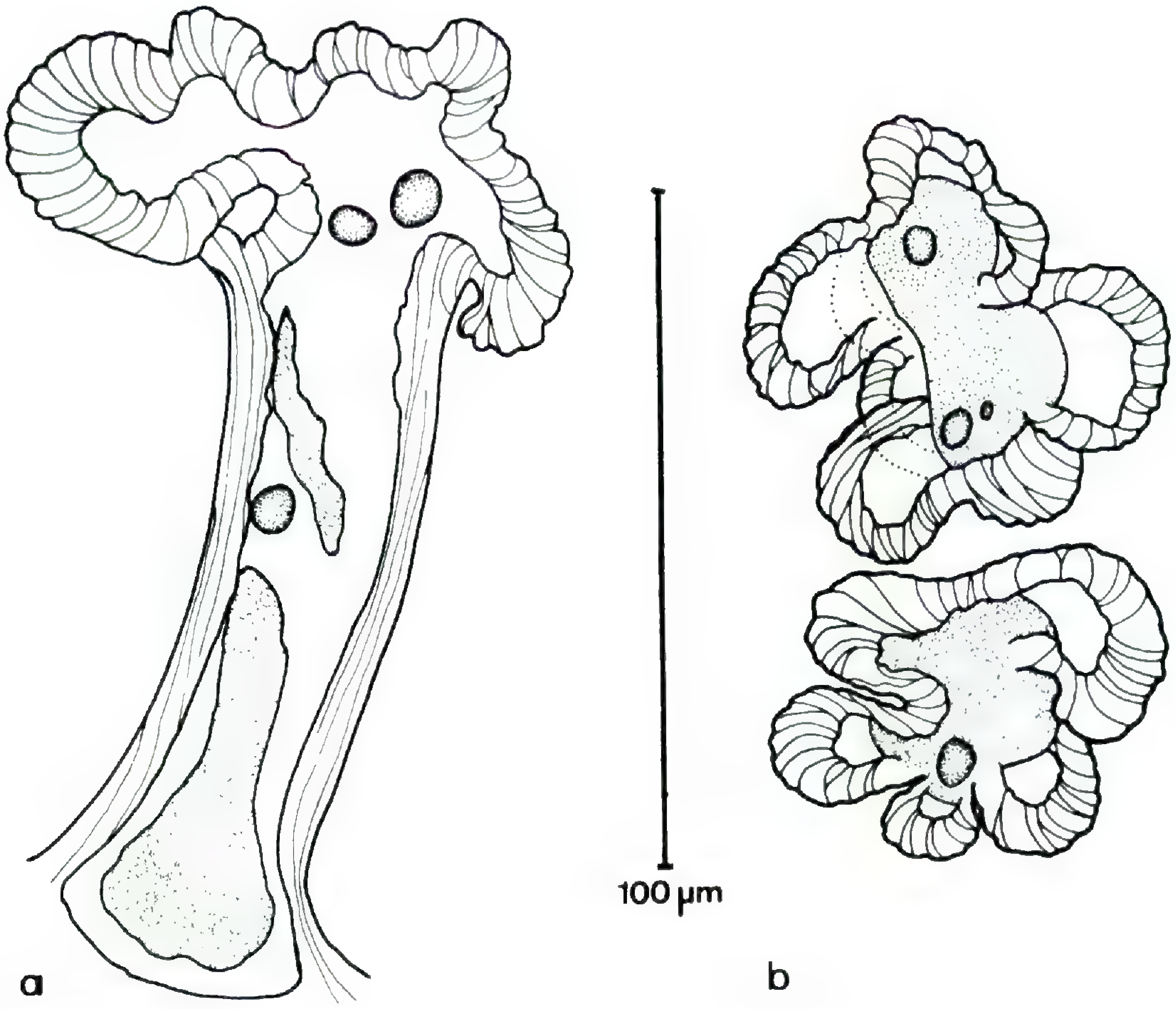

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FIGURE 7.—a. Collector hair in lateral view;—b. Collector hair in apical view.

pollinator. We agree with Mori et al. (1978) that the hood plays a dynamic role in pollination strategies. This structure, besides being the most evident in the floral pattern under both visible and UV light, possesses the greatest concentration of osmophores, which are most conspicuous in the filaments. Pollen from the hood anthers is liberated in tetrads and does not germinate. We classify these as "food" anthers similar to those in *Cassia* and Melastomataceae (Faegri & van der Pijl, 1971).

Flowers are fully open by 3 A.M. However, the first visits of insects begin around 5 A.M., coinciding with the dehiscence of the anthers. The androecial structure creates a microclimate inside the flower. This is characterized by a saturated humidity in the "cup" formed by the androecium of the ring and hood; condensed droplets are easily observed. This saturated microclimate inhibits anther dehiscence and explains the temporal delay between flower opening and dehiscence.

The flower releases a sweet aroma that is strongest in the early morning. The

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FIGURES 1–6.—1. The effective pollinator: *Xilocopa brasilianorum* L. visiting *Couroupita guianensis*; ×0.50.—2. Bees collecting pollen; ×0.50.—3. Starlike stigma; ×33.—4. Longitudinal section of stigma; ×100:—a. collector hairs;—b. papillose cells of the stigmatic tissue.—5. Collector hairs and individual pollen grains; ×400.—6. Individual pollen germinating; ×400.

presence of strong sweet odor in some genera of Lecythidaceae, including *Couroupita*, has been cited by Mori et al. (1978). In order to locate the structures responsible for this odor in *C. guianensis* the Neutral Red method of Vogel (1963) was used. Because the results of this process proved negative, it was necessary to study the internal morphology of the flower in an effort to find the structures responsible for the odor emission. Osmophores are present in the corolla and in the top of the filaments of the hood anthers, in this place they are more conspicuous (Fig. 12–13). The petals and androecium drop off the plant around noontime.

Many classes of insects may visit the flower (bees, wasps, flies and thrips). *Xylocopa brasilianorum* L. is the effective pollinator of *C. guianensis* in the area studied. *Apis mellifera* L. may occasionally act as pollinator, especially when numerous individuals visit the flower simultaneously.

Insect visits begin before sunrise and last until noon; however, it is extremely rare to see *X. brasilianorum* after 10 A.M., behavior that distinguishes it from other bees. The entrance of this bee into the flower is almost always over the frontal part of the hood. This structure functions as a landing platform for *X. brasilianorum*, while many smaller bees land on the ring or on the hood (Figs. 1–2). In order to enter the flower, *X. brasilianorum* pushes the hood down causing a release of pollen tetrads that become attached to the ventral part of the insect. The bee only collects pollen from the hood; during the visit its dorsal part rubs against the anthers of the ring. Under pressure, these latter anthers rotate, facilitating the transfer of pollen from both pollen sacs to the insect body. Pollination occurs when the pollen on the dorsal part of the insects touches the stigmatic area that protrudes above the stamens. This type of pollination is nototrobic. The length of the *X. brasilianorum* visit varies from 30 seconds to 2 minutes.

Apis mellifera behaves in a different manner: it collects pollen during early morning hours from the hood, and later in the day, transfers its attention to the ring and occasionally acts as a pollinating vector. Although many others bees of smaller size visit the flower they never touch the stigma and are considered predators.

GYNOECIUM

STIGMA.—The stigma exhibits a starlike fissure with six to eight points that correspond to the number of carpels (Fig. 3). Two functionally and structurally different tissues of the stigma, both of which participate in the process of fertilization, can be distinguished (Fig. 4):

Collectors and Secretory Hairs: The hairs are unicellular secreting structures with abundant cytoplasm and thick cellulose walls (Fig. 7a). Distally, they broaden irregularly forming an uneven surface with points and protuberances. The hairs form a dense vesture at the edge of fissures that effectively closes the latter during bud development.

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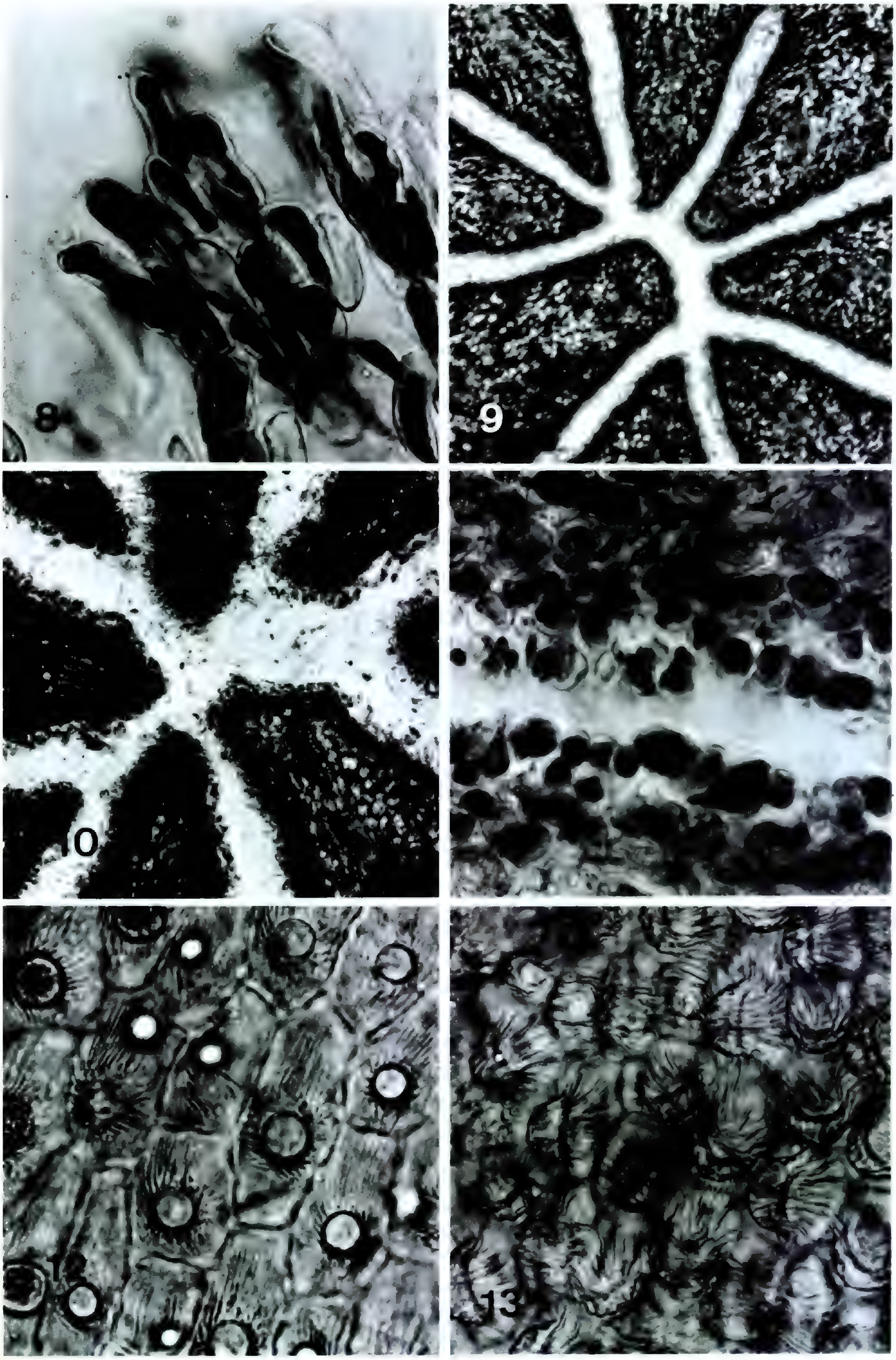
FIGURES 8–13.—8. Top of the transmitting tissue or stigmatic tissue; ×400.—9. Cross section of the style showing canals equal in number equal to the carpels; ×40.—10. Papilionaceous secretory epiderm (transmitting tissue) lining the central canals; ×70.—11. Idem; ×400.—12. The adaxial surface of the corolla—frontal view with oil droplets.—13. Epidermis of the hood filaments; ×160.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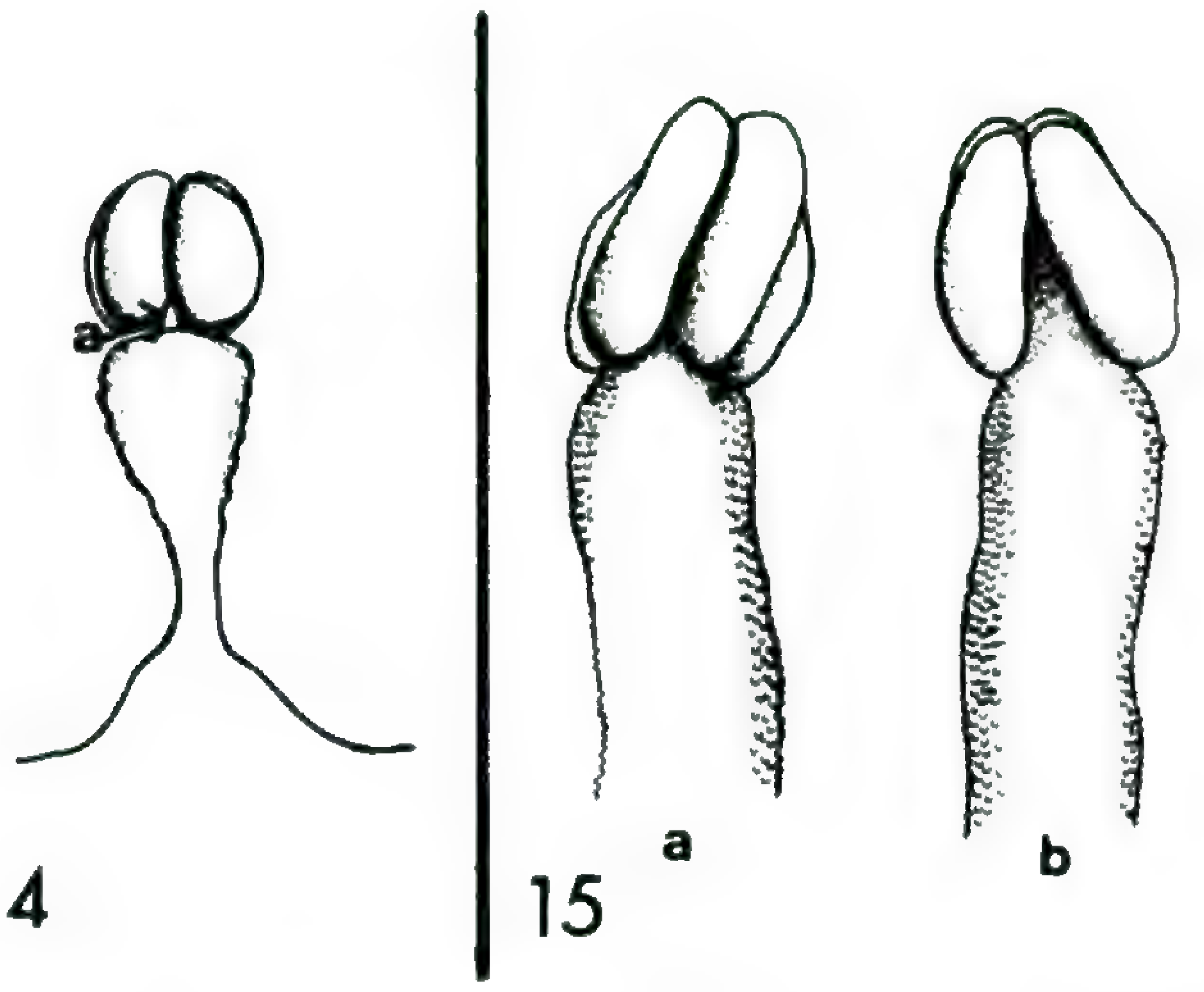

FIGURES 14–15. Stamens.—14. Ring stamen;—a. articulations; ×12.5.—15. Hood stamen;—a. frontal view;—b. dorsal view; ×12.5.

The points and protuberances on the superior part of the hairs considerably increase the stigmatic surface. Oil is exuded through pits at the extreme distal end of the hairs (Fig. 7b). Uphof (1962) classified this type of stigmatal hair as pollen collectors. Pinheiro (1979) ascertained the presence of stigmatic hairs with thickened walls in *Cassia ramosa* Vog. var. *maritima* Irwin which, though lacking secretions, functioned mechanically in the collection of pollen.

Examination of longitudinal and transverse sections of the stigma shows the presence on the stigmatic hairs of a great number of adherent isolated pollen grains and only rarely of pollen tetrads. The position of hood anthers in the flower and the behavior of the pollinator prevent pollen of these anthers from reaching the stigma.

The few tetrads that rarely reach the stigma do not adhere because of the topographically irregular distal portion of the stigma, which effectively excludes the tetrads, and because of the absence of a lipid affinity between the hood pollen and the stigmatic hairs (Figs. 5–6).

Papillose Cells (comprising the top of transmitting tissue or stigmatic tissue).—Stigmatic tissue cells are made up of thin-walled papillose cells with abundant cytoplasm and secretions especially of carbohydrates (Fig. 10). It is on this part of the stigma that the pollen germinates. In other plants, the stigmatic tissue can be found totally exposed, forming stigmatic papillae (Arber, 1937; Martin & Ortiz, 1967; Fahn, 1974; Sedgley & Buthose, 1978).

STYLE.—The style has the shape of a truncated cone with the stigmatic surface at the distal end. It is 0.20–0.25 cm long. Cross sections reveal the continuation of stigmatic fissures of constant width through the style. The fissures are lined with a papilionaceous secretory epiderm which provides nutrients for the development of the pollen tube (Fig. 11). This type of syncarpous gynoecium has been described by Fahn (1974). Canals, equal in number to the carpels, traverse the style, leaving a hollow center (Figs. 9–10).

ANDROECIUM

The androecium is characterized by dimorphic pollen and stamens of the ring and hood.

TABLE 1. Experimental results.

Treatment	No. of Flowers	Pollen Tube Development[a]		% Fruit Set	
		SP	TP	Aborted	Mature
Direct self-pollination	100	§	§	0	0
Indirect self-pollination	100	+	–	85	2
Outbreeding	50	+	–	87	6
Natural pollination	100	+	–	88	4

[a] SP: single pollen. TP: tetrad pollen. §: stigma without pollen. +: with many pollen tubes. –: without pollen tubes.

In the ring, the anther is attached basifixally to a white filament that is 0.15–0.20 cm long. Its dehiscence is longitudinal and, when totally open, the internal surface of the anther is exposed. Articulation of the anther at the point of contact with the filament allows a swiveling movement that facilitates the transfer of pollen to the dorsal part of pollinator (Fig. 14a). Ring pollen is liberated individually. The exine is smooth as noted by Mori & Orchard (1979) and is covered with droplets of lipid substance that adhere to the insect body. Lipid substances facilitate the clustering of pollen grains (Heslop-Harrison, 1971). The lipophilic character of ring pollen and of stigmatic hairs favor the retention of the former in the stigmatic area. The amount of ring pollen with significant protoplasm was estimated at 95%. Culture of this pollen, "in vitro" and "in vivo," resulted in the high percentage of germination of about 80%.

The hood filaments are 0.60–1.0 cm long and are purple at the base and yellow at the apex. The white anther is basifixed and dehisces longitudinally (Fig. 15). In contrast with the ring, hood pollen is dry and has a finely sculptured exine. It is released in tetrads and shed in dense "clouds" soon after the flower opens. The amount of hood pollen with significant protoplasm was estimated at 88%. Nevertheless, in "in vivo" and "in vitro" germinating experiments, not one pollen tube was produced. The ring pollen remains in the anthers until about mid-day, while the hood pollen is released within a few hours after the flower opens. In spite of this, the flower continues to be visited by insects other than the pollinators in search of ring pollen.

These results establish evidence for two physiological pollen types, one fertile and the other providing food for the pollinators (Mori & Orchard, 1979).

REPRODUCTIVE SYSTEM

In order to study the reproductive system of *C. guianensis,* individuals were tested for autogamy, self-compatibility and artificial outbreeding. Beyond contributing to the knowledge of the reproductive system of the family, the tests were undertaken to explain the low incidence of fruit production in relation to the great quantity of flowers.

Observations showed that, although the rate of flower fertilization is high, young fruits are aborted in large numbers (Table 1). A parallel study comparing artificially crossed, self-pollinated and naturally pollinated flowers showed that

there is no difference in the rate of pollen germination or of pollen tube growth in the three situations. The test for direct self-pollination (flowers bagged) did not reveal the presence of pollen on the stigma; otherwise in the other tests pollen tubes are well developed in 45 minutes. By following the development of the pollen tube it was seen that after 24 hours all the tubes had reached at least the base of the ovary and some were already present in the micropyle.

Evidently *C. guianensis* does not present pollen antigen-antibody inhibition in the stigma, style, or ovary, as has been described by Lewis & Crowe (1958). The abortion of so many fruits may be because of the tree's incapacity to support additional fruits.

Flowering occurs from the end of November to mid-May. During 1980 a single tree delayed blossoming until the end of May and subsequently set fruit. This fact and that fruit from experimental autogamy grew normally, led us to conclude that *C. guianensis* is self-compatible; this contradicts Mori & Kallunki's (1976) conclusion. Rather the species is allogamic, which coincides with Prance's (1976) observations.

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A PRELIMINARY NOTE ON POLLINATION IN THE CHENOPODIACEAE

WILL H. BLACKWELL AND MARTHA J. POWELL[1]

Somewhat understandably, interest in pollination biology of members of the Chenopodiaceae has been scant (see Percival, 1965, who made no mention of the family), or else has focused on the "allergic reaction" caused by some members of the family (see Homan, 1963, discussion of *Chenopodium album* as a secondary factor during the ragweed season). Mode of pollination in chenopods is, we believe, open to question in many instances. The general supposition has apparently been that the family is more or less uniformly anemophilous (e.g., Wodehouse, 1935, 1945, 1971), this in association with an abundant, weedy habit. In accordance, Proctor and Yeo (1972) alluded to the significant presence of chenopodiaceous pollen in the "pollen rain." Perhaps the general impression is that chenopods are simply "uninteresting" in terms of pollination biology. However, if some literature is retraced, a rather different perspective may be gained. Volkens (1893) offered the proposition that most members of the family may actually be entomophilous. Knuth (1909) presented what remains as probably the most detailed account of pollination in the Chenopodiaceae, not to mention a number of other families. From his work one is left with the understanding that chenopods are generally either anemophilous or self-pollinated; however, Knuth did not exclude the possibility of insect visits to such taxa as *Salsola kali* L. More recently, Ponomarev and Lykova (1960) credited M. Iljin with the suggestion that entomophily is characteristic of the subfamily Spirolobeae (=Salsoloideae, cf. Blackwell, 1977), admitting, however, that the situation had not been adequately studied. Ponomarev and Lykova further credited Z. P. Bochantseva and T. Vitovich with establishing self-pollination in several taxa of chenopods, including certain species of *Salsola* in Asiatic desert-steppe areas. Ponomarev and Lykova themselves reported the existence of cleistogamy in *Petrosimonia triandra* (Pallas) Simonk and *Salsola brachiata* Pallas. However, they stated that cleistogamous flowers were actually no different structurally from chasmogamous ones, but rather, that the stamens in cleistogamous flowers simply did not become exserted (and consequently would shed pollen internally within the flower). They believed that cleistogamy could be quantified (on a percentage basis) merely by counting the number of flowers with included versus exserted stamens.

From the preceding brief account, it is obvious that pollination biology in the Chenopodiaceae is much in need of investigation, or reinvestigation as the case may be. Such studies might well result in views of pollination mechanisms in the family substantially different from those currently held. Whereas it is probably true that certain major segments of the family, e.g., a number of species of *Atriplex*, are predominantly wind-pollinated systems, anemophily may in fact not prove to be the overpowering rule for the Chenopodiaceae as a whole. Entomophily unquestionably plays a role in some genera. Although entomophily may

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TABLE 1.

Plant Species	Apparent Mode of Pollination	Probable Insect Pollinators
Atriplex canescens (Pursh) Nutt.	Anemophily	———
Halogeton glomeratus (Bieb.) Meyer	Entomophily	Ants: Formicidae
Kochia scoparia (L.) Schrader	Entomophily	Bees: Colletidae and Halictidae
Salsola kali L.	Entomophily	Bees: Colletidae and Halictidae Wasps: Sphecidae
Sarcobatus vermiculatus (Hook.) Torr.	Anemophily	———
Suaeda suffrutescens Wats.	Entomophily	Ants: Formicidae (eyed worker ants), possible aphid relationships Butterflies: Lycaenidae Bees: Colletidae and Halictidae Thrips: Phloeothripidae

well be more common in the Russian thistle subfamily (Salsoloideae), as allegedly indicated by Iljin, it is certainly not excluded from the other subfamily (Chenopodioideae), based for example on our personal observations of insect pollination in *Kochia scoparia* (L.) Schrader. Conversely, anemophily would appear to be the primary method in *Sarcobatus vermiculatus* (Hooker) Torrey, a member of the Salsoloideae. Thus, over-generalizing with regard to subfamily pollination differences would seem unwise at this stage. Self-pollination doubtless occurs here and there throughout the family. However, Proctor and Yeo indicated that sporophytically determined self-incompatibility, an obvious genetic incentive to outcrossing, is known in the Chenopodiaceae. Thus, the matter of cleistogamy in particular should be viewed critically, especially since personal observations indicate that, in *Salsola kali,* the inclusion and exsertion of stamens may be merely a developmental sequence on a given plant. Attempting to quantify "cleistogamy" (as done by Ponomarev and Lykova) would therefore derive statistics that would vary considerably depending on the time of day observations were made.

OBSERVATIONS

The preliminary pollination data presented are based on our field observations made in southeastern Oregon and northwestern Nevada of *Halogeton* (July, 1977), and in Arizona, eastern New Mexico and western Texas (August, 1980) of the other taxa listed (Table 1). These observations were admittedly accomplished during time stolen from other types of projects undertaken on various chenopods. However, care was taken to document the observations photographically and/or by the collection of insect specimens.

THE NEED FOR REASSESSMENT

The Chenopodiaceae would thus seem to provide an unexpectedly interesting source for the investigation of plant/insect relationships, e.g., *Suaeda suffrutes-*

cens with its ant (ant hills close by)–aphid–floral associations. A somewhat unusual feature may prove to be that of relatively large, colorful anthers of some chenopods serving as a primary (or sole) insect attractant (though not necessarily a reward). This is readily observed, for example, in *Salsola kali,* in which the bright yellow anthers become exserted from a small, hyaline, membrane-like perianth, virtually hidden in the leaf axil. Upon anther exsertion, yellow-faced bees (Colletidae) quickly sight the flowers, and progress rapidly from one "exserted" flower to another. Following pollination, the anthers senesce rapidly and turn brown. *Salsola kali,* since it is a weed, is an interesting case because the whole question of pollination in intrinsic versus non-intrinsic ranges comes to bear. *Suaeda suffrutescens* provides an example of red and yellow anther morphs occurring in different flowers. This situation may have potential for experimental studies of pollen load and pollen carry-over. Some *Suaeda* flowers contain a surprising amount of nectar. Studies of nectar volume and sugar concentration could furnish meaningful correlations with an apparent mode of ant pollination. Clearly, a thorough pollination study should be done of as many representative genera and species of the Chenopodiaceae as possible. This is a large, significant family, long neglected with regard to the varied pollination phenomena occurring. Especially interesting would be the investigation of generic (and perhaps specific) pollen design (utilizing SEM) in connection with the precise strategies of pollination in operation. It is hoped that our observations and comments will encourage pollination biologists to take a new look at members of the Chenopodiaceae, and the varied pollination dynamics we believe to exist among them.

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STUDIES IN *IPOMOEA* (CONVOLVULACEAE) I. THE *ARBORESCENS* GROUP[1]

GORDON MCPHERSON[2]

ABSTRACT

The taxon containing the arborescent species of *Ipomoea* is heterogeneous as it is presently recognized. A reclassification of the group has resulted in a taxon that can be characterized by several correlated features (involving habit, inflorescence type, sepal size, shape, texture, and pubescence, corolla color and pubescence, and seed pubescence) in contrast to its historical antecedent. The relationships of the ten constituent species are briefly discussed, and a detailed key and complete descriptions incorporate my conclusions concerning the limits of these species.

Despite the long history and general acceptance of the taxon historically ancestral to it, the group comprising the arborescent species of *Ipomoea* and their close relatives has not been accurately circumscribed and the boundaries of its constituent species remain inadequately defined. As one result of a study of most of the species of *Ipomoea* in Mexico and Central America, I now recognize a taxon, the *Arborescens* group, which includes many of the erect, woody species traditionally considered closely related but excludes certain others. The composition suggested below permits the recognition of the group on a broader morphological basis than previously, and brings into association with the arborescent species certain woody vines.

Choisy (1845) recognized the group "*Arborescentes*" and defined it as the subsection of the erect species (section *Orthipomoea*) of *Ipomoea* that are arborescent. In this subsection he placed *I. murucoides, I. arborescens, I. batatilla, I. haenkeana,* and *I. coriacea.* House (1908), in treating the North American species of the genus, added *I. fistulosa* (a synonym of *I. carnea*), *I. glabriuscula, I. nicaraguensis, I. cuernavacensis, I. intrapilosa, I. calva,* and *I. wolcottiana.* Matuda (1964), in dealing with the genus as it is represented in Mexico, added *I. chilopsidis* and *I. pauciflora* to the list of arborescent species, and he placed *I. wolcottiana* into synonymy with *I. pauciflora.* O'Donell (1950) added *I. calodendron* and *I. vargasiana* from Peru, and commented that the group is "de sistematica bastante confusa."

Among the names in the above roster, there are several that do not belong there. *Ipomoea coriacea* Choisy is a Brazilian species described as having herbaceous to membranous sepals, purple corollas, and glabrous seeds in contrast to the coriaceous sepals, white corollas, and pilose seeds of the *Arborescens* group. Therefore, although I have not seen the type, I have no hesitation in regarding this species as misplaced among those of the *Arborescens* group. *Ipomoea glabriuscula* House, although described by House as a tree, is in fact a vine closely related to and perhaps synonymous with *I. microsticta* Hallier f., as

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Williams (1970) has pointed out. My study of the type specimen confirms his conclusion. *Ipomoea carnea* Jacq. and *I. haenkeana* Choisy are distinctive, usually shrubby species that are properly placed in another group of species of which *I. jalapa* (L.) Pursh is typical. *Ipomoea carnea* lacks such key features of the *Arborescens* group as the inflorescence of one (or rarely few) flowers, the adaxially much-pubescent sepals, the marginally long-pilose seeds, and the white corolla. It resembles *I. jalapa* in its corolla and seed pubescence, its large inflorescence, and its calyx morphology. Similarly the Brazilian *I. haenkeana* deserves to be disassociated from the tree species and to be placed near *I. durangensis* House of the *Jalapa* group because of its corolla color and pubescence, its short-petiolate leaves, and its sepal morphology.

Ipomoea fistulosa is merely a synonym for the twining form of the widespread and variable *I. carnea*, as Verdcourt (1963) first suggested. Austin (1977) agreed with him, and furthermore rightly sank into synonymy the names *I. batatilla* House and *I. nicaraguensis* (H.B.K.) G. Don. The description of the former species contains no characteristics that do not fall easily within the variation exhibited by *I. carnea*. Of the latter I have seen the type (Valles de Aragua, Caracas, Cumana, *Humboldt & Bonpland s.n.* (P, holotype)).

With the exclusion of *I. haenkeana, I. glabriuscula,* and *I. carnea* and its synonyms, the "*Arborescentes*" becomes more homogeneous. The group must, however, be expanded to include four species, three of which were hitherto not associated with any of its elements. Two of these, *I. populina* and *I. praecana,* probably owe their previous independence to their vining habit, which distinguishes them from the rest of the *Arborescens* group. In the diagnostically important features, however, they closely resemble the tree species. The third new inclusion is a recently described tree species, *I. teotitlanica,* and the fourth is *I. pulcherrima* van Ooststroom, a little known species from Peru.

The thirteen resulting names are reduced to ten when three of them are relegated to various synonymies in the discussion to follow.

The group is plainly a derived one within the genus. Its pseudoracemose inflorescence is formed by the gathering on reduced branches of usually one-flowered cymes, and its arborescent habit depends upon an anomalous type of wood formation (Lujan, 1974). Because of the apparent relationship of the group to two other groups of which *I. jalapa* and *I. pedicellaris* are representative, (McPherson, in prep.), it may be speculated that among the ancestors of the *Arborescens* group was a pubescent vine with ovate leaves and a strongly pubescent corolla. This description also applies to *I. praecana,* and this species can furthermore be regarded as morphologically central within the group, related on the one hand to *I. arborescens* and on the other to *I. murucoides,* and through them to the rest of the species. These two species, alone among those of the *Arborescens* group, resemble *I. praecana* in their dense sepal and corolla pubescence.

Related to *I. arborescens* are *I. wolcottiana, I. pauciflora* and *I. populina,* which are alike in having reduced corolla pubescence, smaller, sometimes squat sepals, and shortened adaxial sepal pubescence. Unique to this trio is the possession of cylindrical stigmas 1.5 to 3 times as long as wide. To my knowledge the stigmas of all other *Ipomoea* species are globose; the character is a useful

one for rapidly distinguishing *Ipomoea* from such other superficially similar genera as *Convolvulus*. The linking of these three species with *I. arborescens* depends upon the close similarity of *I. wolcottiana* with the latter species. In some incomplete collections only the very fine nature of the adaxial sepal hairs, a condition presumably derived from that of *I. arborescens*, allows accurate discrimination of the two. *I. pauciflora* and *I. populina* are also very similar; indeed the only character that allows identification of certain glabrous extremes of *I. populina* is its twining habit. This habit must be regarded as secondarily derived if the arrangement of species proposed here is accepted.

The remaining four species seem most nearly similar to *I. murucoides*. *Ipomoea teotitlanica* resembles it in leaf pubescence, sepal pubescence and texture, and in the tendency of the sepals to lack adaxial hairs. *Ipomoea intrapilosa* differs from *I. murucoides* mainly by its near lack of any pubescence except that on the adaxial surface of the sepals. *Ipomoea chilopsidis* is also principally distinguished from *I. murucoides* by its nearly glabrous condition, but is additionally more narrowly leaved. Many collections of *I. murucoides* indicate that that species has a tendency to develop narrow leaves, as well. The closest relationship of *I. chilopsidis* is therefore with either *I. murucoides* or *I. intrapilosa*. The little-known *I. pulcherrima* appears to be most similar to *I. teotitlanica* because of its glabrous sepals and corolla, and its orbicular, densely pubescent leaves.

Taxonomy

Trees or woody vines. Pubescence soft. Leaves entire, large, ovate-lanceolate, linear or orbicular, truncate or cordate at the base, often absent at the time of flowering. Inflorescence reduced to 1–2 (rarely –5)-flowered cymes typically more or less clustered on a reduced shoot into a pseudoraceme. Peduncles short, the pedicels exceeding them (often greatly so). Sepals large (mostly 10–28 mm long), ovate with obtuse-mucronate apices, mostly pubescent on the adaxial surface and often on the abaxial surface, coriaceous, about equal. Corolla white, large (5–9 cm long), twisted in bud, mostly pubescent on the interplical regions. Seeds long-pilose on the dorsal margins, otherwise glabrous.

Key to the Species of the *Arborescens* Group

Specimens of these species are often difficult to identify because they frequently flower and fruit while leafless. Moreover, they exhibit considerable variation in size of floral parts, as well as in density of pubescence. This key attempts to take into consideration these problems. Provision is also made for those specimens for which the habit is neither obvious nor stated by the collector.

1a. Plants vining.
- 2a. Sepals, leaves, and stems tomentose-woolly, sometimes glabrescent; sepals 15–25 mm long. .... 7. *I. praecana*
- 2b. Sepals, leaves, and stems glabrous or merely pubescent; sepals 5.5–10 mm long. .... 6. *I. populina*

1b. Plants erect, or habit unknown.
- 3a. Youngest stems pubescent, sometimes eventually glabrescent, but then retaining some pubescence in sheltered places on the most recent growth.
  - 4a. Sepals 14–28 mm long (if 14 mm long, then rarely less than 10 mm wide at the base); corolla usually pubescent over most of the exterior surface.

5a. Stem villous and glabrescent; leaves at least twice as long as wide, truncate at the base; tree. .... 4. *I. murucoides*
5b. Stem densely tomentose; leaves about as wide as long, cordate at the base; vine. .... 7. *I. praecana*
4b. Sepals 5.5–15(–17) mm long (if over 14 mm long, then 5–8 (rarely –10) mm wide); corolla pubescent only at the tips and/or along the margins of the interplical regions, or glabrous.
6a. Hairs of the stem straight to curved, mostly erect, 0.5 mm long or longer; hairs of the corolla restricted to the margins of the interplical regions or absent in some specimens; vine; Guerrero to Chiapas and Central America. .... 6. *I. populina*
6b. Hairs of the stem more or less curly, somewhat matted, usually less than 0.5 mm long; hairs of the corolla on the tips of the interplical regions as well as on the margins, or absent in two species (one Peruvian and one known only from northern Oaxaca); trees; throughout Mexico, as well as further south.
7a. Corolla glabrous; leaves orbicular or broadly ovate; adaxial surface of the sepals glabrous or bearing curly hairs up to 0.7 mm long.
8a. Sepals 11–16 mm long; northern Oaxaca. .... 9. *I. teotitlanica*
8b. Sepals 5–10 mm long; Peru. .... 8. *I. pulcherrima*
7b. Corolla pubescent; leaves ovate to lanceolate; adaxial surface of the sepals bearing straight hairs up to 0.5 mm long.
9a. Adaxial surface of the sepals densely puberulent with hairs ca. 0.1 mm long; stamens 1.2–2.8 cm long; flowering pedicels 6–17(–19) mm long; fruiting pedicels 16–27(–30) mm long; central and southern Mexico. .... 10. *I. wolcottiana*
9b. Adaxial surface of the sepals pubescent with hairs 0.25 mm long or longer; stamens 3–4 cm long; flowering pedicels (13–)15–30 mm long; fruiting pedicels (13–)15–45 mm long; central and northern Mexico. .... 1. *I. arborescens*
3b. Youngest stems glabrous, even in sheltered places.
10a. Leaves very narrow (rarely to 1 cm wide). .... 2. *I. chilopsidis*
10b. Leaves wider (rarely less than 3 cm wide) or absent from the specimen.
11a. Sepals 13–19 mm long, glabrous abaxially, the outer sepals usually bearing hairs up to 0.5 mm long on the adaxial surface (rarely completely glabrous). .... 3. *I. intrapilosa*
11b. Sepals 5–14(–16) mm long, glabrous or pubescent abaxially (if glabrous abaxially, then 10 mm long or less; if 13 mm long or longer, then pubescent or puberulent at least at the base), the outer sepals bearing hairs rarely up to 0.3 mm long on the adaxial surface.
12a. Trees.
13a. Sepals pubescent or puberulent abaxially, at least at the base. .... 10. *I. wolcottiana*
13b. Sepals glabrous abaxially. .... 5. *I. pauciflora*
12b. Plants of unknown habit.
14a. Sepals glabrous abaxially; corolla glabrous on the tips and margins of the interplical regions (compare also with *I. populina*). .... 5. *I. pauciflora*
14b. Sepals pubescent or puberulent abaxially (usually); corolla usually pubescent on the tips and/or margins of the interplical regions.
15a. Adaxial surface of the sepals densely puberulent with fine, tiny hairs; stamens 12–28 mm long. .... 10. *I. wolcottiana*
15b. Adaxial surface of the sepals pubescent with coarse, bulbous-based hairs; stamens 10–13 mm long. .... 6. *I. populina*

1. Ipomoea arborescens (Humb. et Bonpl. ex Willd.) G. Don, Gen. Syst. 4:267. 1838.

Convolvulus arborescens Humb. et Bonpl. ex Willd., Enum. 1:204. 1809. TYPE: Between Acaguisotla and Chilpancingo, *Humboldt & Bonpland s.n.* (P, holotype).

Argyreia (?) *oblonga* Benth., Bot. Voy. Sulphur 133. 1845. TYPE: Tepic, *Hinds* (?) *s.n.* (BM, holotype, not seen; K, isotype).

Ipomoea murucoides var. *glabrata* Rose, Contr. U.S. Natl. Herb. 1:107. 1891. TYPE: *Palmer 316* (1890) (US, holotype).

Trees 5–15 m tall, the trunks up to 50 cm in diameter, the bark light colored. Stems producing a white latex, usually tomentose when young, with usually curly and somewhat matted hairs 0.10–0.25 mm long, glabrescent by the third year, often ridged or sulcate longitudinally on drying. Leaf blades entire, 9–19 cm long, 6–9 cm wide, with 12–18 lateral veins on each side of the midrib, ovate to lanceolate, acuminate at the apex, cordate at the base, usually tomentose [the hairs 0.1–0.3(–0.7) mm long with tiny swollen bases] especially on the lower leaf surface and on the veins of the lower leaf surface, often rendering that surface grey green as opposed to the green of the upper leaf surface, sometimes sparsely pubescent and at maturity bearing hairs only on the veins and along the margin, or rarely (*McVaugh & Koelz 1582*) glabrous at maturity. Blades often biglandular at the base of the midrib beneath with glands 1–2 mm long, or bearing (nectariferous?) projections less than 1 mm long. Petioles 1–9 cm long, usually tomentose with curly hairs up to 0.4 mm long.

Inflorescences terminal or axillary, each cyme consisting of 1 (or rarely 2) flowers, these reduced cymes usually borne on shortened, tomentose, ridged branches 1–14 cm long. Peduncles 0.3–1.0 cm long, tomentose; secondary peduncles (if present) 2–4 mm long, tomentose. Bracts 4–6 mm long, 2–3 mm wide, ovate-lanceolate to hemispherical, tomentose on the abaxial surface, tomentose or glabrous on the adaxial surface, caducous. Pedicels 1.5–4.5 cm long, thicker at the apex than at the base, often sulcate on drying, tomentose, thickening in fruit. Sepals 6–14 mm long, 6–8 mm wide (the outer the same size as, or slightly larger than the inner), ovate or occasionally suborbicular, obtuse or obtuse-mucronate at the apex, tomentose abaxially at least where exposed, tomentose on the margins and on the adaxial surface at least along the midline with hairs 0.25 mm long or longer, the abaxial surface often pitted or wrinkled. Corolla 4–6 cm long, 4–6 cm in diameter, slightly twisted in bud, funnelform, tomentose without on the tips of the interplicae, tomentose or sericeous along their margins, white with greenish tube, the interplical regions cream, the throat reddish or purplish within. Stamens 25–40 mm long, the anthers 4–8 mm long, the basal hairs up to 5 mm long, gland tipped. Style 20–30 mm long, the basal 1–2 mm thickened and persistent, the stigmas 2, globose, 2–2.5 mm long. Capsule 2-locular, 4-valved, the valves 17–25 mm long; seeds pilose on the dorsal margins with hairs 10–15 mm long.

Ipomoea arborescens inhabits open thorn forests, oak savannas, and dry deciduous forests. Its distribution is indicated in Fig. 1. This species grows at elevations of 50 to 1800 m and usually flowers and fruits between November and April.

MEXICO. SONORA: Las Durasnillas, 18 May 1892, *Brandegee s.n.* (UC); 0.3 miles SE of La Noria, *Carter et al. 71–35* (UC); San Bernardo, Río Mayo, *H. S. Gentry 1158* (MO) and *1277* (MICH); Sierra de Alamos, *H. S. Gentry 3000* (MO, UC, US) and *H. S. Gentry 4888* (MICH, MO); Arroyo Cuchuhuaqui, near Alamos, *H. S. Gentry 876M* (DS); near Alamos, *Rose 12815* and *12882* (US); Alamos, 26 Mar–8 Apr 1890, *Palmer 316* (US); Alamos, *Goldman 291* (US); Bacatejaca, *Hartman 268* (UC); Baromena, *H. S. Gentry 6127* (MICH); 18 miles S of Moctizuma, *Wiggins 7439* (MICH); above

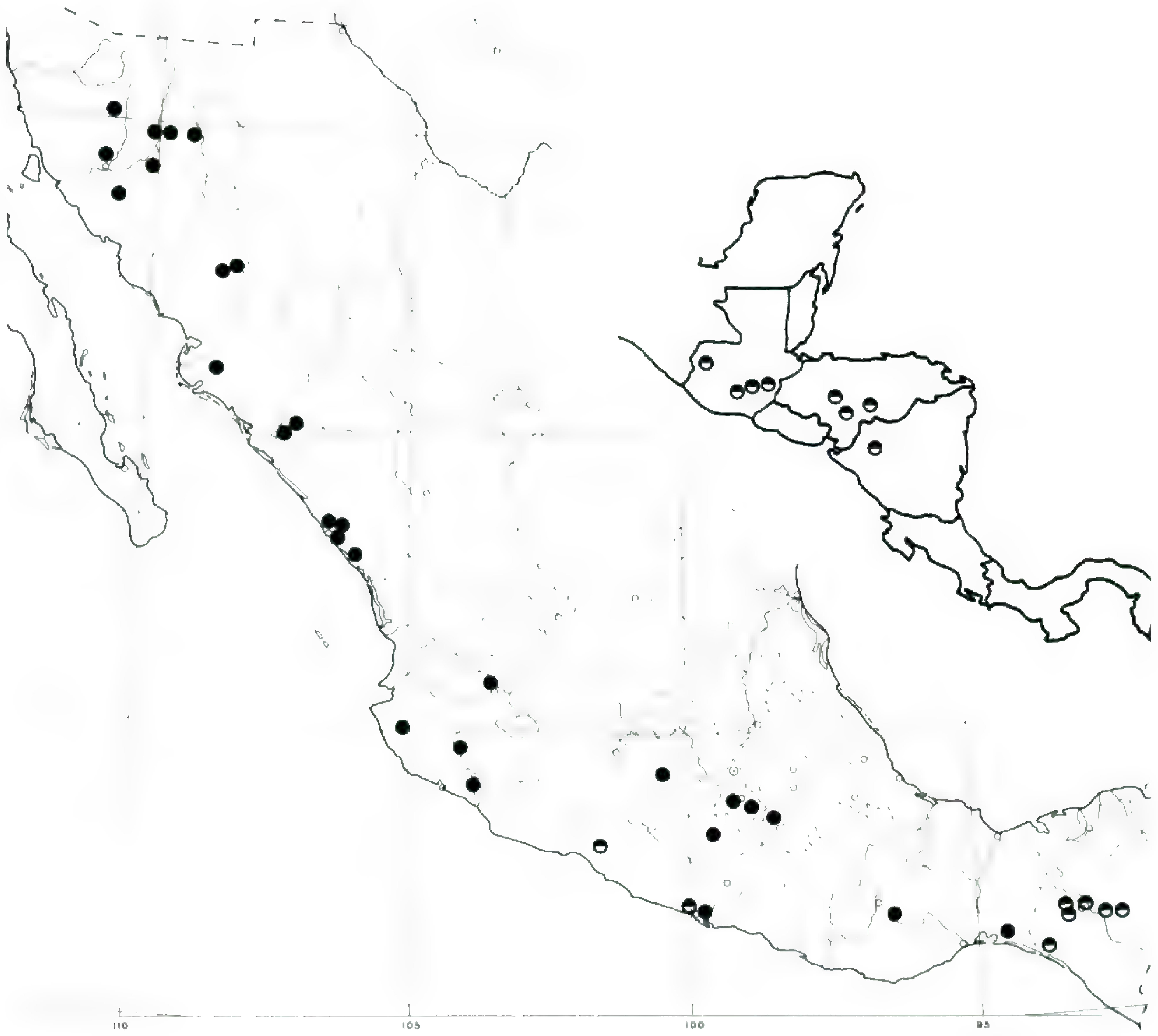

FIGURE 1. Distribution of *Ipomoea arborescens* (solid circles) and *I. populina* (half circles).

Fabrica de Los Angeles, *Wiggins 7291* (MICH); between Bacadéhuachi and Granados, *White 2923* (MICH); canyon W of Río Sonora, Baviácora, *Drouet, Richards, & Lockhart 3623* (DS); near Torres, *Coville 1662* (US); 22 miles N of Hermosillo, *Moran 9971* (US). SINALOA: Culiacán, 25 Oct 1904, *Brandegee s.n.* (UC); NE of Los Mochis on road to Choix, *Carter & Kellog 3254* (MICH, US); Mesa Malqueson, Cerro Colorado, *H. S. Gentry 5158* (MO, UC); Imala, *H. S. Gentry 4976* (MICH, MO); 10 km E of Concordia, *McVaugh 23583* (MICH); 3 miles W of Concordia, *Graber 7* (MICH); Rosario, *Rose 1409* (US) and *Rose 14529* (US); *Montes & Salazar 173* (US); Mazatlán, *Ortega 4956* (US); Balboa, *Ortega 5034* (US). JALISCO: 10–13 km SE of El Tuito, *McVaugh 25414* (MICH); between La Huerta and Autlán, *Templeton 9485* (MICH); La barranca, Guadalajara, *M. E. Jones 27317* (DS). COLIMA: 11 miles SSW of Colima, *McVaugh & Koelz 1582* (MICH). MICHOACÁN: Zitácuaro, *Hinton 13562* (MICH, MO, US). GUERRERO: Iguala, *Goodding 2190* (UC). MORELOS: near Cuernavaca, *Rose 6863* (US); Yautepec, *Rose 5339* (US). OAXACA: 2 km S of Niltepec, *King 1766* (MICH); S of Mitla, *Ernst 2294* (US). PUEBLA: 5 km S of Izúcar de Matamoros, *Henrickson 2087* (MICH).

2. Ipomoea chilopsidis Standley, Field Mus. Nat. Hist., Bot. Ser. 17:206. 1937. TYPE: *H. S. Gentry 2391* (F, holotype, not seen; MO, UC, US, isotypes).

Shrubs 2–5 m high. Stems broadly ridged on drying, glabrous. Leaf blades entire, 10–20 cm long, 0.5–1.3 cm wide, with 18–30 lateral veins on each side of the midrib, linear, acute at the apex, acute at the base, glabrous. Blades biglandular at the base of the midrib beneath with glands ca. 1 mm long. Petiole 0.5–1.2 cm long, glabrous.

Inflorescences terminal on unreduced branches, each cyme consisting of 1(–3) flowers. Peduncles in the axils of unmodified leaves, 0.4–2.2 cm long, glabrous. Bracts unknown, caducous. Pedicels 1.5–2.5 cm long, somewhat ridged on drying, glabrous. Sepals coriaceous, 12–16 mm long, 7–9 mm wide, equal in size or the outer slightly smaller than the inner, ovate, obtuse or acute at the apex, glabrous abaxially, coarsely short-pubescent adaxially over the entire surface, the hairs less than 0.10 mm long. Corolla 8–9.5 cm long, 8–9 cm in diameter, strongly twisted in bud, funnelform, glabrous, white with purple throat. Stamens 50–55 mm long, the anthers 8–9 mm long, the basal hairs 1–1.5 mm long, gland tipped. Capsule 2-locular, 4-valved, the valves 18–20 mm long; seeds 4, long-pilose on the dorsal margins and also sparsely so on the ventral margin with hairs about 10 mm long.

The rarely collected *I. chilopsidis* flowers between July and September and is described by the collector of the type as "singularly of the high and arid crags." Its known distribution is indicated in Fig. 2.

MEXICO. CHIHUAHUA: La Bufa, SE of Creel, *Knobloch 516* (MICH); Mpio of Batopilas, E of La Bufa, *Bye 7738* (MICH); Guasaremos, Rio Mayo, *H. S. Gentry 2391* (type) (MO, UC, US); SW Chihuahua, Aug–Nov 1885, *Palmer 297* (US).

3. **Ipomoea intrapilosa** Rose, Gard. & Forest 7:367. 1894. Syntypes: *Palmer 703* (1886) (US), *Pringle 2443* (DS, MICH, US). *Palmer 703* (1886) (US) is here designated as the lectotype.

I. murucoides var. *glabrata* A. Gray, Proc. Amer. Acad. Arts 22:440. 1887. TYPE: *Palmer 703* (1886) (GH, holotype, not seen; US, isotype).

Trees 3–10 m high, the trunks up to 50 cm in diameter, the bark light colored. Stems producing a white latex, ridged on drying, glabrous. Leaf blades entire, 7–14 cm long, 3–5.5 cm wide, with 10–17 lateral veins on each side of the midrib, lanceolate to narrowly ovate, acuminate at the apex, truncate or shallowly cordate at the base, glabrous or sparsely pubescent on the lower surface near the base of the midrib. Blades sometimes biglandular at the base of the midrib beneath with glands ca. 1 mm long, or more often bearing (nectariferous?) projections up to 1 mm high instead. Petioles 3–9 cm long, glabrous.

Inflorescences terminal or axillary, each cyme consisting of 1–3(–5) flowers, these reduced cymes often borne on shortened, glabrous, ridged branches, which sometimes bear reduced leaves. Peduncles 0.4–2.0 cm long, glabrous, darkened and often ridged on drying. Bracts 3–6 mm long, 1–2.5 mm wide, ovate to oblong, glabrous on both surfaces or pubescent within, caducous. Flowering pedicels 1.8–4.0 cm long; fruiting pedicels 3.0–5.0 cm long, darkened and ridged on drying, thickening distally, glabrous. Sepals coriaceous, 13–19 mm long, 7–13 mm wide (about equal in size or the outer slightly smaller than the inner at fruiting), ovate, obtuse or obtuse-mucronate or acute at the apex, the abaxial surface glabrous, usually wrinkled on drying, the adaxial surface of at least the outermost sepals bearing long (0.25–0.5 mm), soft, straight, appressed hairs (rarely all 5 sepals with the adaxial surface smooth and glabrous). Corolla 5–8 cm long, 5–7 cm in diameter, funnelform, glabrous or sparsely pubescent along the margins of the interplical regions, white or yellowish white, the tube and the interplical regions greenish yellow. Stamens 3–4 cm long, the anthers 8–10.5 mm long, the basal

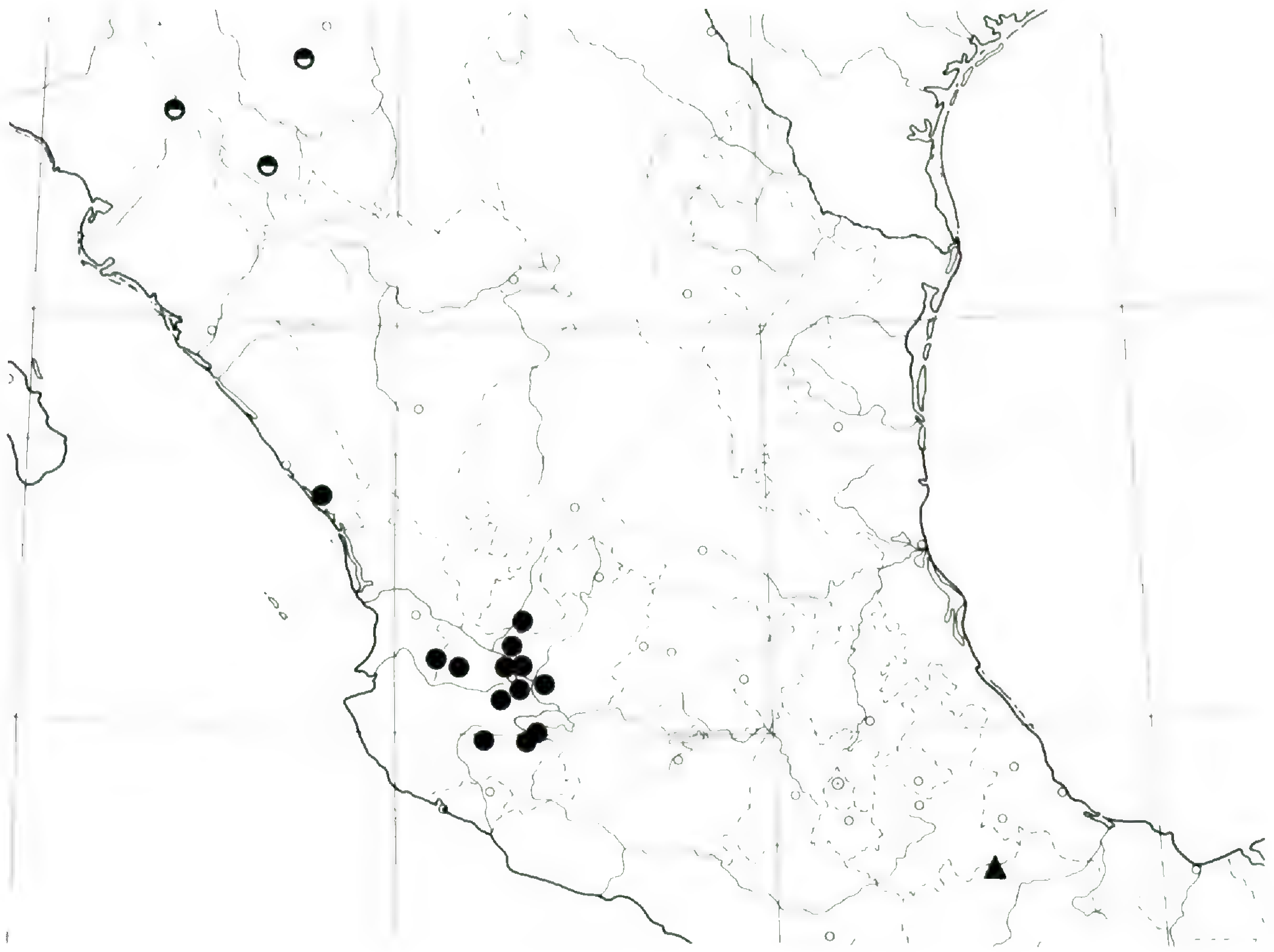

FIGURE 2. Distribution of *Ipomoea chilopsidis* (half circles), *I. intrapilosa* (solid circles), and *I. teotitlanica* (triangle).

hairs up to 2.5 mm long, gland tipped. Style 3.5–4 cm long; stigmas 2, globose to slightly elongate, 1 mm long. Capsule 2-locular, 4-valved, the valves 2–2.5 cm long; seeds 4, pilose on the dorsal margins with hairs 10–15 mm long.

Ipomoea intrapilosa inhabits dry shrublands, oak forests and tropical deciduous woodlands. Its distribution is indicated in Fig. 2. This species grows at elevations of 900 to 2200 m and flowers and fruits between October and April.

MEXICO. ZACATECAS: 8 miles S of Moyahua, *Webster 1092* (MICH). SINALOA: Near Colomos, foothills of Sierra Madre, *Rose 1680* (US). NAYARIT: Ixtlán, *H. S. Gentry 6814* (MICH). JALISCO: 6–7 km E of Plan de Barranca, *McVaugh 23507* (MICH); Guadalajara, *Boutin 2116* (MICH); near Guadalajara, *Pringle 2443* (MICH, MO, UC, US); 5 km NE of Guadalajara, *McVaugh 23503* (MICH); between Guadalajara and San Luis Soyatlán, *Templeton 9410* (MICH); 37 miles N of Guadalajara, *Hess & Hall 620* (MICH); 25 miles SW of Guadalajara, *McVaugh 13304* (MICH); Baños de Oblatos, S slope of barranca near Guadalajara, *Moran 14710* (MICH); 40 km SW of Guadalajara, *McVaugh 24429* (MICH); near Guadalajara, *Safford 1420*; between Copimatlán and Tizapán, *Templeton 9442* (MICH); 17 km N of Zapotlanejo, *Rzedowski 15640* (MICH); Ixtlahuacán de los Membrillos, *Detling 8701* (MICH) and *Detling 8749* (MICH); barranca S of Rio Verde, *McVaugh & Koelz 249* (MICH); Chapala, Oct–Nov 1886, *Palmer 703* (type) (US); near Chapala, *Rose 7689* (US); Cuesta de San Marcos, 15 km SSE of Acatlán de Juarez, *McVaugh & Koelz 321* (MICH); S of Jocotepec, *Frye 3014* (UC).

4. **Ipomoea murucoides** Roem. & Schult., Syst. Veg. 4:248. 1819. TYPE: not determined ("e horto valentino").

Convolvulus macranthus H.B.K., Nov. Gen. Sp. 3:95. 1819. TYPE: Guanaxuato, *Humboldt & Bonpland s.n.* (P, holotype).

Ipomoea macrantha (H.B.K.) G. Don, Gen. Syst. 4:267. 1838, not *I. macrantha* Roem. & Schult., Syst. Veg. 4:251. 1819.

Trees 3–13 m high, the trunks up to 40 cm in diameter, the bark light colored. Stems producing a white latex, floccose or tomentose when young with somewhat matted hairs up to 1.3 mm long, glabrescent in exposed places. Leaf blades entire, 9–20 cm long, 1–7 cm wide, with 12–22 lateral veins on each side of the midrib, lanceolate, elliptical or linear, acuminate at the apex, truncate at the base, variously pubescent, usually villous with hairs 0.5–1.3 mm long at least when young, often partially or completely glabrescent at maturity, the hairs remaining longest on the lower surface along the veins and in their axils with the midrib. Blades often biglandular at the base of the midrib beneath with glands ca. 1 mm long, or bearing (nectariferous?) fingerlike projections 0.5–1.5 mm long. Petioles 1–6 cm long, tomentose, often glabrescent.

Inflorescences terminal or axillary, each cyme reduced to 1(–2) flowers, the reduced cymes usually borne on a shortened, villous branch in the axils of closely spaced, somewhat reduced leaves, these often fallen at flowering. Peduncles 0.2–2.0 cm long, or if bearing more than one flower, up to 2.5 cm long, densely villous. Bracts 10–19 mm long, 5–10 mm wide, villous abaxially, more densely so adaxially, caducous. Pedicels 1.5–5 cm long, densely villous, usually longitudinally grooved on drying, gradually thickened distally. Sepals coriaceous, 14–28 mm long, 9–20 mm wide (the outer usually ca. 5 mm longer than the inner), ovate to broadly oblong, obtuse or acute at the apex, villous abaxially and usually at least partially so adaxially, the marginal ⅔ of the inner sepals often glabrous and smooth abaxially, the outer sepals partially glabrescent abaxially. Corolla 5–8 cm long, 5–9 cm in diameter, funnelform, twisted in bud, villous at least along the apical margins of the interplical regions and often over most of the exterior, white with some dull red or purple in the throat, the interplical regions and the tube greenish or yellowish white without. Stamens 25–40 mm long, the anthers 9–10 mm long, the basal hairs 1.5–3 mm long, gland tipped. Style 25–40 mm long; stigmas 2, globose 1–1.5 mm long. Capsule 2-locular, 4-valved, the valves 20–25 mm long, 4-seeded; seeds pilose on the dorsal margins with hairs 10–18 mm long.

Ipomoea murucoides is a relatively common species inhabiting dry, thorny shrublands and sparse, deciduous forests, as well as roadsides and dry, cut-over woodland-pastures. Its distribution is indicated in Fig. 3. This species grows at elevations of 600 to 2400 m and usually flowers and fruits between October and April.

MEXICO. DURANGO: 36 miles S of Cd. Durango on road to Mesquital, *H. S. Gentry 22090* (US); 40–60 miles SSE of Cd. Durango on road to Mezquital, *Maysilles 7413* (MICH). NAYARIT: Near Jesús Maria, *Feddema 1302* (MICH); SW of Yxtlán, *Mexia 800* (MICH, MO, UC). JALISCO: 10 km NW of Huejuquilla, *Rzedowski 17625* (MICH); 7 miles N of Colotlán, *Webster 12* (MICH); 5 miles E of Atotonilco, *Moldenke 1663* (MICH); about 10 km SW of Villa Guerrero, *McVaugh 25811* (MICH); 5 miles SW of Huacasco, *McVaugh 11994* (MICH); 12 miles SE of junction at Lagos de Moreno (near road to León, Gto), *McVaugh 17794* (MICH); Cerro Gordo, 12 miles SE of Tepatitlán, *McVaugh 17490* (MICH); Jocotepec, *H. S. Gentry 6813* (MICH); 12–13 km from Amacueca towards Tapalpa, *McVaugh 25957* (MICH); 10 km N of Sayula, *Iltis 816* (MICH); 8 miles S of Autlán toward La Resolana, *Wilbur 2399* (MICH). ZACATECAS: On road to Huejuquilla el Alto, 1 mile W of road junction 18 miles S of Valparaíso on road to Mezquitic, *McVaugh 17720* (MICH); about 15 km NE of Huejuquilla el Alto, *McVaugh 25716* (MICH); 8–15 km W toward Tlaltenango from road junction W of Jalpa, *McVaugh 25659* (MICH). GUANAJUATO: Salvatierra, *Rzedowski 26972* (MICH). AGUASCALIENTES: 12 miles W of Aguascalientes, *McVaugh 23792*. QUERETARO: Tetillas, *Kelly 650* (MICH,

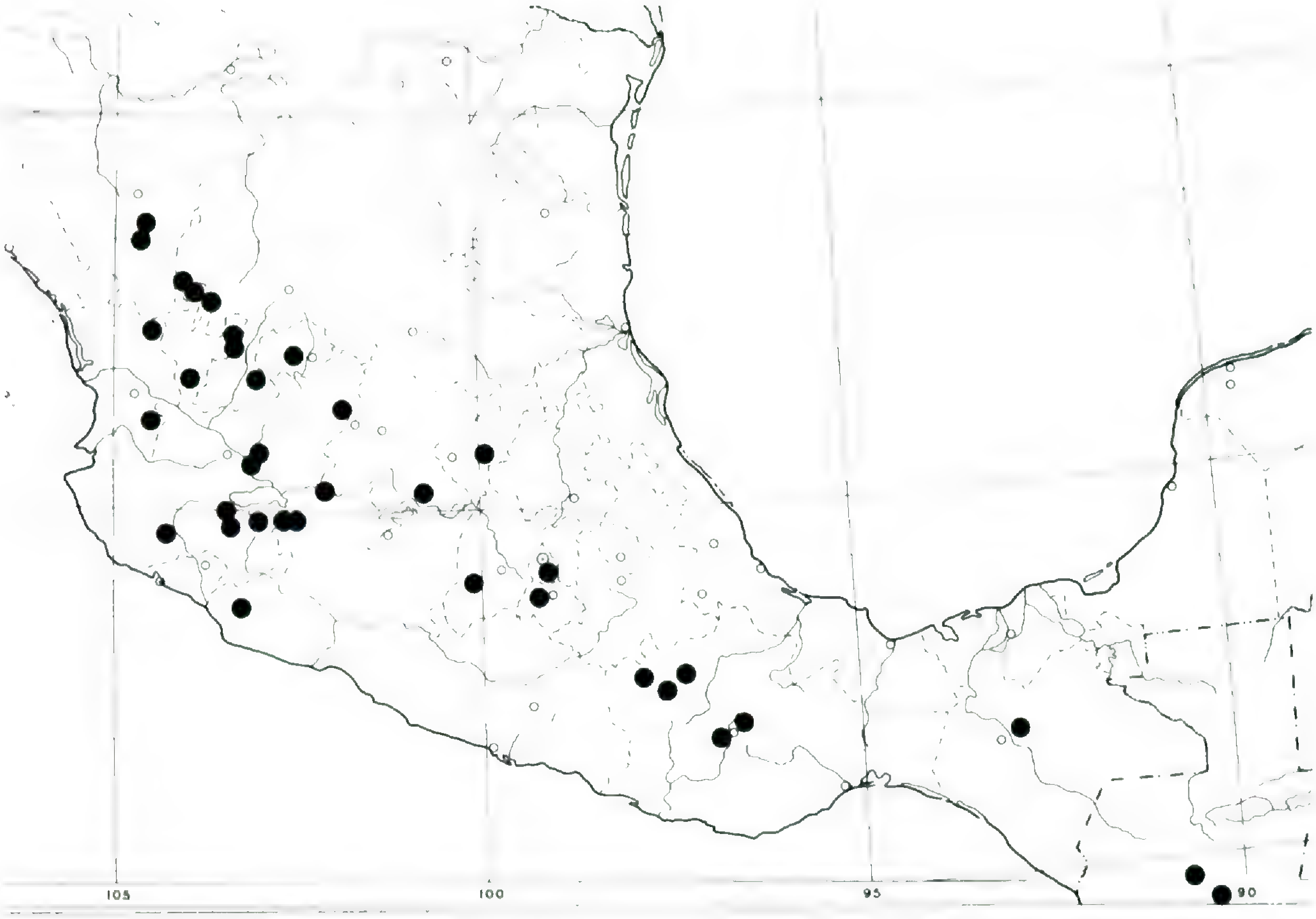

FIGURE 3. Distribution of *Ipomoea murucoides*.

UC); 2 miles S of Cavillo, *McVaugh & Koelz 60* (MICH). MICHOACÁN: 17 miles W of Jiquilpan, *McVaugh 21968* (MICH); 5 miles N of Cotija and 22 miles S of Jiquilpan, Cerro Potrerillos, *King & Soderstrom 4597* (MICH); 3 km E and 8–10 km NE of Cotija de la Paz, *McVaugh 24930* (MICH); Coalcomán, *Hinton 12692* (MICH); 1 mile E of Iratzio, *Weber & Charette 11861* (UC); La Piedad, *Moldenke 1666* (MICH). MORELOS: Near Nepantla, *Converse 38* (MICH, UC); near Cuernavaca, *Lemmon 209* (UC). MEXICO: Salitre, District of Temascaltepec, *Hinton 8730* (MICH). DISTRITO FEDERAL: Hill E of Shrine of Guadalupe, *Alexander & Hernandez X. 4* (MICH); Sierra de Guadalupe, extreme S of Cerro del Risco, *Rzedowski 23498c* (MICH). OAXACA: 20 km S of Huajuapan de León, *Funk 2373* (MICH); valley of Oaxaca, *Pringle 6066* (MICH, MO, UC); 6–8 miles NE of Cd. Oaxaca, *H. S. Gentry 12072* (MICH); Albán, near Oaxaca, *Messer 152* (MICH); 8 km NW of Tamazulapan, *McVaugh 22477* (MICH); 4 km W of Magdalena Jicotlán, *Cruz C. 2649* (MICH, MO); Cerrado San Filipe, *Langman 3488* (US). PUEBLA: Near San Luis Tultitlánapa, near border with Oaxaca, *Purpus 3531* (MICH, UC); ladera E of Cerro Tecajete, near San Miguel Papaxtla, *Rzedowski 24916* (MICH). CHIAPAS: 5 km above Soyaló along road to Bochil, *Breedlove 21298* (MICH, MO).

GUATEMALA. Santa Rosa, *Heyde & Lux 4733* (MICH); near Antigua, *Standley 60312* (MICH).

5. Ipomoea pauciflora Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 12:266. 1845. TYPE: *Galeotti 1403* (BR, holotype, not seen; P, presumed isotype).

Key to the Subspecies

1a. Peduncles 3–12 mm long; Mexico, Guatemala. .... 5a. subsp. *pauciflora*
1b. Peduncles 2–30 mm long; Peru. .... 5b. subsp. *vargasiana*

5a. I. pauciflora Mart. & Gal. subsp. **pauciflora**

Trees or shrubs 3–8 m high, the trunks up to 25 cm in diameter, the bark light brown, the branches disposed to twining. Stems producing a white latex, glabrous, usually strongly ridged on drying. Leaf blades entire, 5–15 cm long, 3–8.5

cm wide, with 10–15 lateral veins on each side of the midrib, ovate, acuminate at the apex, truncate or shallowly cordate at the base, glabrous on both surfaces. Blades often biglandular at the base of the midrib beneath with glands less than 1 mm long, or bearing (nectariferous?) projections less than 1 mm long. Petioles 3–8 cm long, glabrous.

Inflorescences terminal or axillary, each cyme consisting of 1–5 flowers, the cymes borne on shortened, glabrous, ridged branches which sometimes bear reduced leaves. Peduncles 0.3–1.2 cm long, glabrous. Bracts triangular, 1.5–3 mm long, ca. 1–1.5 mm wide, glabrous, caducous. Flowering pedicels 0.8–3.0 cm long; fruiting pedicels 2.0–3.9 cm long, both usually ridged on drying, gradually thickening distally, glabrous. Sepals coriaceous, 5–9 mm long, 6–9.5 mm wide, ovate to oblong, obtuse (and usually mucronate) or acute at the apex, glabrous abaxially, densely pubescent adaxially (at least near the apex) with squat, broad-based hairs up to 0.3 mm long, often only the bulbous bases well developed. Corolla 6–8 cm long, 5–11 cm in diameter, funnelform, glabrous, white with deep red or purple throat. Stamens 9–11 mm long, the anthers 5–7.5 mm long, the basal hairs up to 2 mm long, gland tipped. Style 6–8 cm long; stigmas 2, cylindrical, 2.5–3 mm long, 1–2 mm wide. Capsule 2 (or rarely 3)-locular, 4-valved, the valves 17–22 mm long; seeds 4 (or rarely 5), pilose on the dorsal margins with hairs 10–14 mm long.

Ipomoea pauciflora subsp. *pauciflora* inhabits sparse, low woodlands and deciduous forests as well as roadsides. Its distribution is indicated in Fig. 4. This subspecies grows at altitudes of 400 to 2000 m and usually flowers and fruits between September and February.

MEXICO. MICHOACÁN: 50 km N of Arteaga, *McVaugh 22528* (MICH); La Florida, District of Zitácuaro, *Hinton 13406* (GH, MICH, US). GUERRERO: Near Acapulco, Oct 1894–Mar 1895, *Palmer 619* (MICH). MORELOS: S of Cuernavaca at km 79 marker on road to Acapulco, 24 Sep 1964, *Palacios s.n.* (MICH); S of Cuernavaca at km 93 marker on road to Acapulco, 25 Nov 1964, *Palacios s.n.* (MICH); Cuernavaca, *Rose 4339* (US) and *Rose 6965* (GH, US); Cuernavaca, *Lemmon 210* (GH, UC); E of Cuernavaca, *Dunn 18615* (NY); plain below Cuautla, *Converse 37* (UC). MEXICO: Pungenancho, District of Temascaltepec, *Hinton 7404* (MICH, US); Temascaltepec, *Hinton 8754* (GH, US). OAXACA: 8 km NW of Tamazulapan, Mpio of Huajuapan, *McVaugh 22478* (MICH); near Mitla, *Messer 56* (MICH) and *Messer 255* (MICH); N of San Miguel de Valle, *Schoenwetter JSOX-131* (US); Monte Albán, *Pringle 4965* (NY, UC); 32 miles SE of Oaxaca, *Webster 11653* (GH); floodplain of Río Atoyac near Oaxaca, *Camp 2435* (NY); Comaltepec, *Liebmann 12474* (GH); *Galeotti 1403* (type) (P). PUEBLA: 8 km SE Tehuitzingo on road to Acatlán, *Rzedowski 19298* (MICH); near Tehuacán, *Rose 9905* (US) and *Rose 11393* (US); 8 miles N of Tehuacán, *Anderson 5323* (MICH); 18 miles N of Tehuacán, *H. S. Gentry 20215* (US); near Pueblo Nuevo, S of Coxcatlán, *Smith & Tejeda 4508* (US); near San Luis Tultitlanapa, *Purpus 3532* (UC); Amatitlan, *Miranda 2256* (GH); 18–20 km from Oaxaca border on road from Huajuapan de León to Izúcar de Matamoros, *Anderson 5651* (MICH). VERA CRUZ: Chapulco, *Liebmann 12465* (UC). CHIAPAS: Near Monte Bonito, Mpio of Arriaga, *Ton 3380* (MICH); along Mex 190 in the Zinacantan paraje of Muctajoc, Mpio of Ixtapa, *Breedlove 13817* (MICH).

GUATEMALA. Near Zacapa, *Pittier 1762* (US).

5b. I. pauciflora Mart. & Gal. subsp. **vargasiana** (O'Donell) McPherson, comb. nov.

I. vargasiana O'Donell, Bol. Soc. Peruana Bot. 1:5. 1948. TYPE: *Vargas 1021* (not seen).

Trees or shrubs to 7 m tall. Stems ridged on drying, glabrous. Leaf blades entire, 6–10 cm long, 3.5–8 cm wide, with 11–14 lateral veins on each side of the midrib, ovate, acuminate at the apex, shallowly cordate at the base, glabrous on both

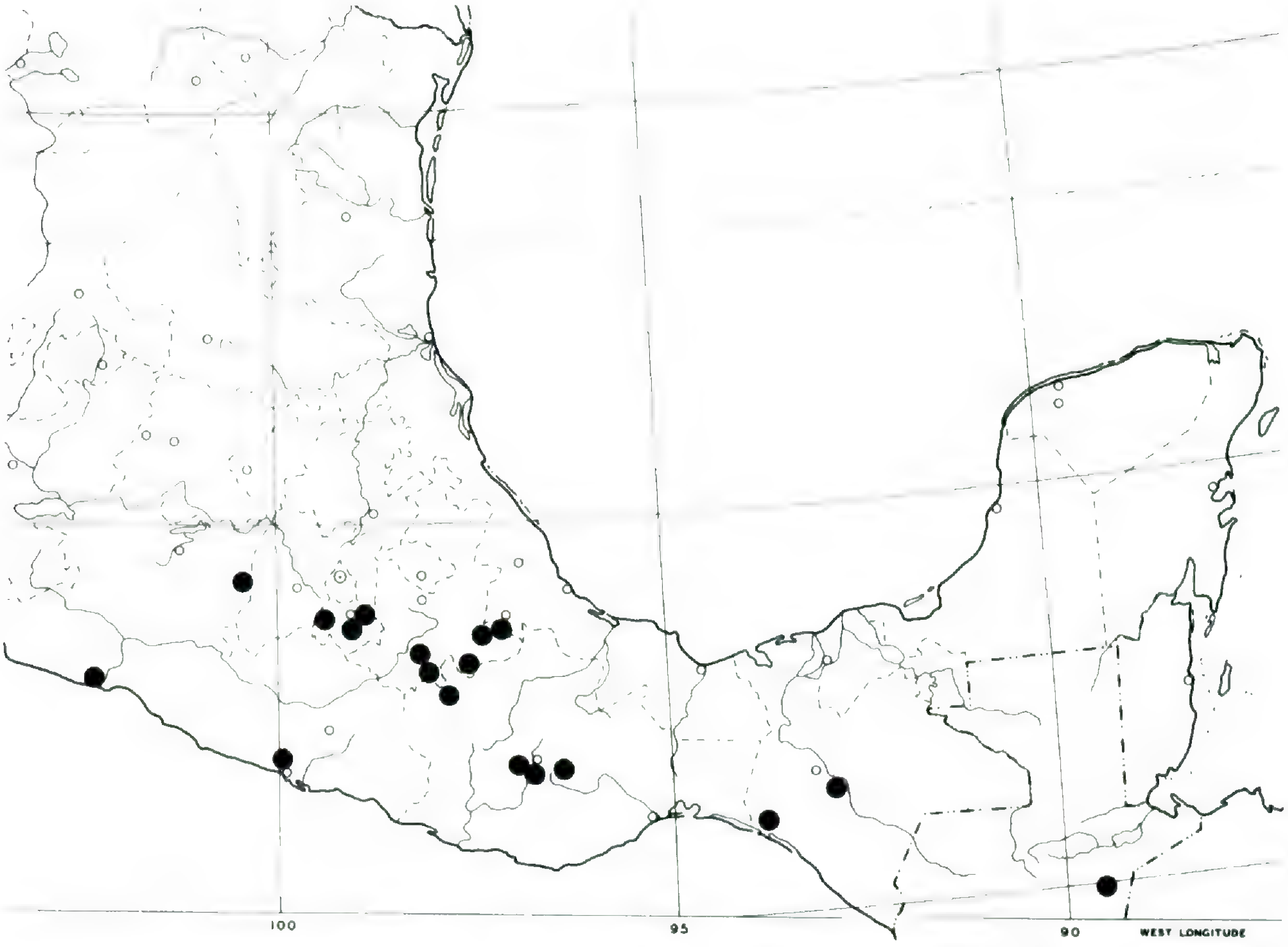

FIGURE 4. Distribution of *Ipomoea pauciflora* subsp. *pauciflora* in Mexico and Central America.

surfaces. Blades often bearing 2 (nectariferous?) projections up to 1 mm long at the base of the midrib beneath. Petioles 1.5–9 cm long, glabrous.

Inflorescences terminal or axillary, each cyme consisting of 1–3 flowers, the cymes usually borne on shortened, glabrous branches on which the subtending leaves are somewhat reduced or absent. Peduncles 0.2–3.0 cm long, glabrous, ridged and darkened on drying. Bracts ca. 3 mm long, 1 mm wide, oblong, glabrous, caducous. Pedicels 2.0–3.0 cm long, slender, sometimes thickened distally, ridged and darkened on drying, glabrous. Sepals coriaceous, 7–11 mm long, 6–9 mm wide, broadly ovate, acute at the apex, somewhat auriculate at the base, glabrous abaxially, densely strigose adaxially with squat hairs up to 0.1 mm long including the swollen, papillalike base. Corolla 5–7 cm long, 6–7 cm in diameter, funnelform, glabrous, white. Stamens 11–12 mm long, the anthers 6–8 mm long, the basal hairs to 1 mm long, gland tipped. Style ca. 6 cm long; stigmas 2, cylindrical, ca. 2 mm long, 1 mm wide. Capsule 2-locular, 4-valved, the valves over 12 mm long; seeds unknown.

These plants grow at elevations of 400 to 2600 m and flower and fruit in May and June.

This subspecies is only weakly distinguished from the typical subspecies. The chief difference is the sometimes greater length of the peduncles of subsp. *vargasiana*. Therefore, recognition of the two taxa as separate species seems quite inappropriate, despite their wide disjunction. In fact, were it not for this disjunct distribution, the Peruvian populations might not be recognized at all.

PERU. AYACUCHO: between Ayacucho and Huanta, *Weberbauer 5665* (US) (det. O'Donell); below Huanta, *Weberbauer 5667* (US) (det. O'Donell). APURIMAC: Apurimac, *Weberbauer 5899* (US) (det. O'Donell). ABANCAY: Limatambo, *Balls 6838* (F, US) (det. O'Donell).

6. **Ipomoea populina** House, Ann. New York Acad. Sci. 18:226. 1908. TYPE: *Palmer 482* (1894–1895) (NY, holotype).

Woody vines or prostrate trailers to 4 m long (probably reaching greater lengths), once recorded as an "arching shrub." Stems ridged and grooved on drying, glabrous or pubescent with somewhat curly hairs to 0.8 mm long. Leaf blades entire, 4.5–13 cm long, 3–9 cm wide, with 9–14 lateral veins on each side of the midrib, ovate to ovate-lanceolate, acuminate at the apex, truncate or somewhat cordate at the base, usually pubescent at least on the lower surface near the junction with the petiole, sometimes fairly densely pubescent on both surfaces, or sparsely pubescent beneath, or glabrous (the amount of pubescence often varying on one plant, as it does on the type collection), the hairs up to 0.8 mm long, usually somewhat curly. Blades often biglandular at the base of the midrib beneath with glands 1 mm long, or bearing (nectariferous?) projections ca. 1 mm long.

Inflorescences terminal or axillary, each cyme consisting of 1–5 flowers, these reduced cymes usually borne on shortened, glabrous or pubescent, often ridged branches up to 9 cm long. Peduncles 0.3–2.6 cm long, often ridged and darkened on drying, glabrous or pubescent. Bracts 2–4 mm long, 1–1.5 mm wide, triangular to oblong, glabrous, caducous. Pedicels 1.3–3.5 cm long, thickened distally (sometimes only slightly), ridged and darkened on drying, glabrous or pubescent. Sepals coriaceous, 5.5–12 mm long, 6–9 mm wide (the outer usually slightly smaller than the inner), ovate to broadly ovate to suborbicular, acute or obtuse at the apex, often somewhat auriculate at the base, glabrous or sometimes pubescent on the apical half, the abaxial surface usually wrinkled on drying, the adaxial surface covered with coarse, bulbous-based, appressed hairs up to 0.2 mm long. Corolla 5.5–8(–10) cm long, 7–11 cm in diameter, funnelform, usually sparsely pubescent especially along the margins of the interplical regions, but often glabrous, white with a purple throat. Stamens 10–13 mm long, the anthers 6–7 mm long, the basal hairs up to 1.5 mm long, gland tipped. Style ca. 5 mm long, the basal 2 mm thickened and persistent; stigmas 2, cylindrical, 2–3 mm long, 1 mm wide. Capsule 2-locular, 4-valved, the valves 15–25 mm long, 4-seeded; seeds long-pilose along the dorsal margins, the hairs 10–15 mm long.

Ipomoea populina inhabits tropical deciduous forests as well as cut-over areas, roadsides, and riverbanks. Its distribution is indicated in Fig. 1. This species grows at elevations of 200 to 2000 m and usually flowers and fruits between November and January.

MEXICO. GUERRERO: Acapulco and vicinity, Oct 1894–Mar 1895, *Palmer 482* (type) (GH, NY, UC, US); Sierra Madre of Michoacán and Guerrero, *Langlassé 612* (US); Montes de Oca, *Hinton 11528* (MICH, NY, US). CHIAPAS: Mpio of Ocozocoautla de Espinosa, near Derna, *Breedlove 30290* (UC); between Hacienda Juncaná and San Vicente, *Nelson 3509* (US); between Chiapa de Corzo and Tuxtla Gutiérrez, *Breedlove 22952* (MICH); El Chorreadero, 5.6 miles E of Chiapa de Corzo, *Breedlove 9561* (F); 13 km N of Arriaga, *Breedlove 30544* (UC); 8 km SW of Berriozábal, *Breedlove 23054* (MICH).

GUATEMALA. Agua Caliente and Sanarate, *Holway 856* (US); near Río Hondo, Zacapa, *Williams*

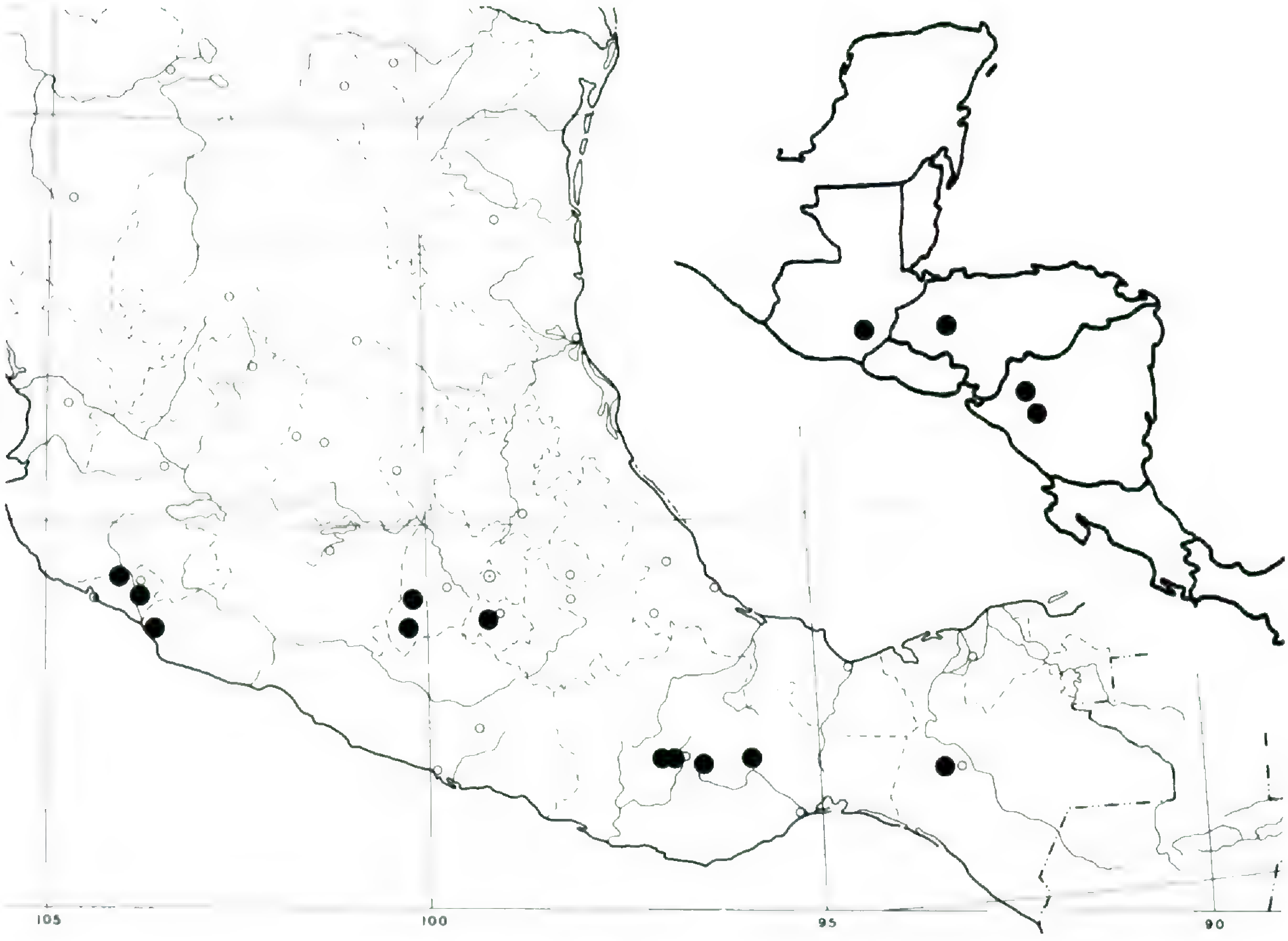

FIGURE 5. Distribution of *Ipomoea praecana*.

41887 (NY); Guatemala City, *Popenoe 360a* (US); 40 km NW of Huehuetenango, *Williams 41308* (US); Cuilco, Huehuetenango, *Shannon 415* (US); near Zacapa, *Pittier 1762* (NY).

HONDURAS. Between Tegucigalpa and El Picacho, *Molina R. 8785* (US); 20 km S of Tegucigalpa, *Molina R. 18464* (NY); near San Francisco, Rio Yeguare valley, *Williams 11481* (GH).

NICARAGUA. 3–7 km NW of Pueblo Nuevo, Estelí, *Williams 42423* (US); 15 km N of Estelí, *Williams 20209* (NY).

7. Ipomoea praecana House, Ann. New York Acad. Sci. 18:227. 1908. TYPE: *Nelson 1823* (GH, presumed holotype; US, presumed isotype).

Trailing or clambering woody vines or sprawling shrubs to 10 m long. Stems often longitudinally ridged, short-tomentose with hairs 0.25 mm long. Leaf blades entire, 8–23 cm long, 9–21 cm wide, with 8–12 lateral veins on each side of the midrib, ovate to orbicular, acuminate at the apex, cordate at the base, pubescent above, at least on the main veins, densely tomentose beneath with hairs up to 1 mm long, often the lower surface grey green. Blades biglandular at the base of the midrib beneath with glands 1–2 mm long. Petioles 4–11 cm long, short-tomentose.

Inflorescences terminal or axillary, the 1-flowered cymes often borne in dense clusters on reduced, sometimes short-branched axes which occasionally bear reduced leaves, these axes 2–6 cm long, often ridged, pubescent like the stem. Peduncles 0.3–0.8(–10) cm long, densely tomentose. Bracts 10–20 mm long, 4–6 mm wide, densely tomentose on both surfaces, caducous. Pedicels 1.3–3.5 cm

long, usually markedly grooved longitudinally on drying, densely tomentose. Sepals coriaceous, 15–25 mm long, 10–15 mm wide (the outer equal to or slightly larger than the inner), ovate, obtuse at the apex, often longitudinally grooved on drying, densely tomentose abaxially, usually partially tomentose adaxially near the apex, the hairs up to 0.3 mm long. Corolla 6–12 cm long, 7–10 cm in diameter, funnelform, pubescent over most of the outer surface, the hairs occasionally arising in pairs, white within the interplical regions yellowish white without. Stamens 30–45 mm long, the anthers 10–12 mm long, the basal hairs 1–2 mm long, gland tipped. Style ca. 40 mm long; stigmas 2, globose, ca. 1.5 mm long. Capsule 2-locular, 4-valved, the valves 18–24 mm long, 4-seeded; seeds pilose on the dorsal margins and sometimes also on the ventral margin, the hairs 10–20 mm long.

Ipomoea praecana is known from tropical deciduous forests, especially dry oak forests. Its distribution is indicated in Fig. 5. This species grows at elevations of 150 to 1300 m and flowers and fruits between September and March.

MEXICO. COLIMA: 9–10 km E or SE by winding road from Minatitlán, *McVaugh 26236* (MICH); 11 miles SSW of Colima, *McVaugh & Koelz 1567* (MICH); 17–18 km SSW of Colima on the Manzanillo road, *McVaugh 22972* (MICH). MICHOACÁN: 3–6 km SE of San Juan de Lima, *McVaugh 22994* (MICH); 5 km N of Cruz de Campo, *Dieterle 3176* (MICH). MORELOS: Near Cuernavaca, *Pringle 7229* (GH). MEXICO: Guayabal, District of Temascaltepec, *Hinton 8739* (F, MO, US). OAXACA: Between Alanoloyas and Santa Catarina, *Conzatti 1656* (GH); near Reyes, *Nelson 1823* (type) (GH, US). CHIAPAS: Mpio of Ocozocoautla de Espinosa, near Derna, *Breedlove 30288* (DS); Mpio of Terán, Crispin, *Breedlove 30365* (DS); Escuintla, *Matuda 582* (MICH); 5.6 miles SE of Chiapa de Corzo on Mex 190, *Ton 3257* (MICH); above El Chorreadero, Mpio of Chiapa de Corzo, *Breedlove 23044* (DS, MICH).

GUATEMALA. Department of Jalapa, *Kellerman 5645* (US).

HONDURAS. Oturo valley, Department of La Paz, *Molina R. 23332* (F).

NICARAGUA. S of Darío, Matagalpa, *Seymour & Atwood 2595* (MICH); 3–7 km NW of Pueblo Nuevo, Estelí, *Williams 42419* (US).

8. Ipomoea pulcherrima van Ooststroom, Recueil Trav. Bot. Néerl. 30:206. 1933. TYPE: *Weberbauer 5875* (B, holotype, not seen; GH, US, isotypes).

Trees or shrubs. Stems producing a white latex, ridged on drying, densely puberulent with curly hairs up to 0.2 mm long, the older stems partially glabrescent. Leaf blades entire, 5–9 cm long, 4–8.5 cm wide with 8–12 lateral veins on each side of the midrib, broadly ovate to orbicular, obtuse at the apex, subcordate or truncate at the base, pubescent above with very slender, more or less appressed hairs 0.2–0.5 mm long, much more densely pubescent beneath (the lower surface completely obscured and appearing much lighter than the upper) with similar hairs. Midrib apparently not glandular. Petioles 1.5–3.5 cm long, densely puberulent like the stem.

Inflorescences terminal or axillary, each cyme consisting of 1 (or rarely 2) flowers, these reduced cymes often borne on shortened, puberulent branches up to 3 cm long. Peduncles 0.2–0.4 cm long, densely puberulent. Bracts ovate, 1.5–2 mm long, 1 mm wide, glabrous or puberulent abaxially on the midrib, caducous. Pedicels 0.8–1.4 cm long, puberulent, ridged on drying. Sepals unequal (the outermost 5–6 mm long, 4–5 mm wide, the innermost 9–10 mm long, 6–7 mm wide), broadly oblong, glabrous on the abaxial surface and apparently also on the adaxial surface. Corolla 4–5 cm long, ca. 2.5 cm in diameter, funnelform, glabrous, prob-

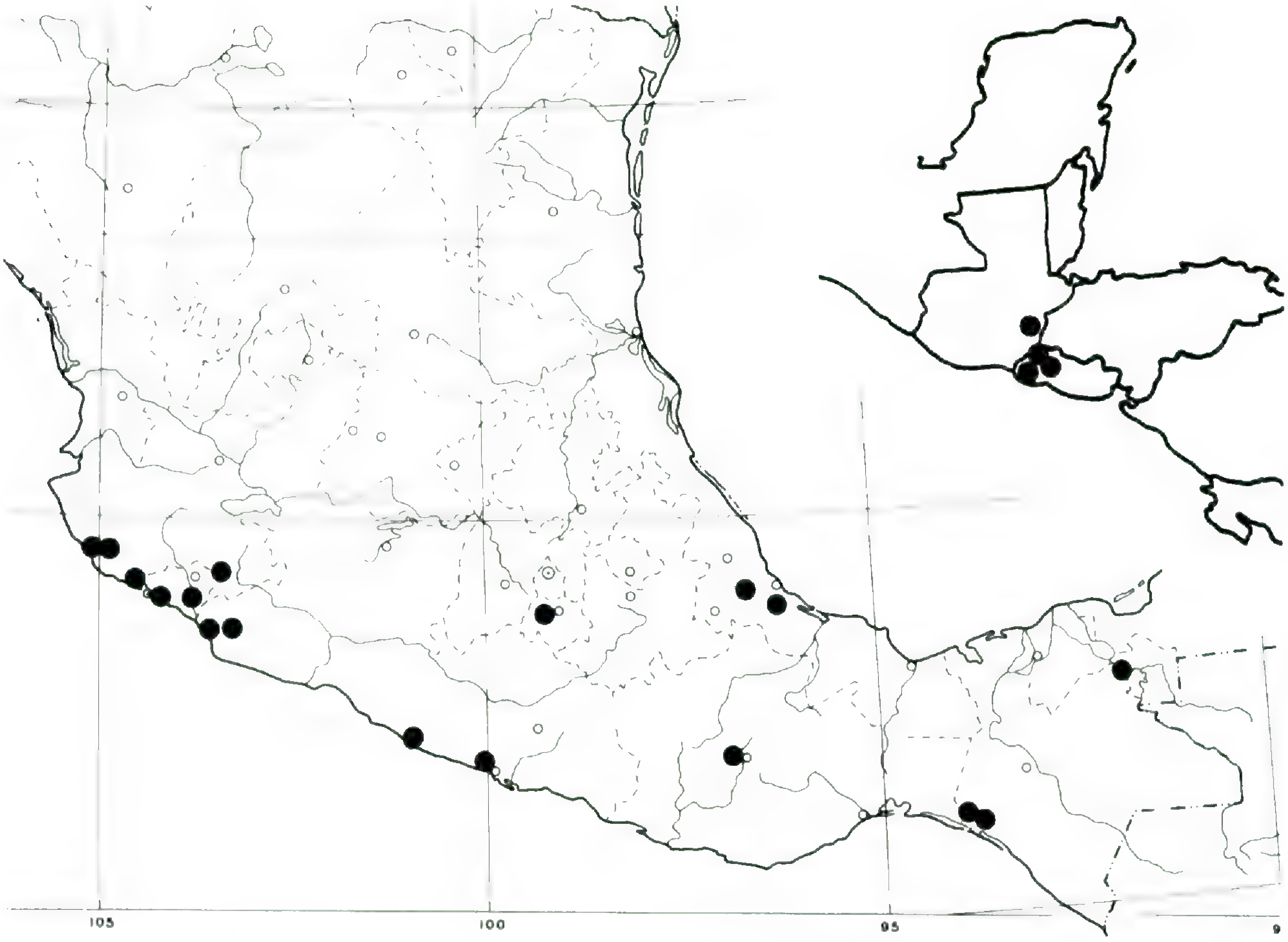

FIGURE 6. Distribution of *Ipomoea wolcottiana* subsp. *wolcottiana* in Mexico and Central America.

ably white. Stamens 18–25 mm long, the anthers 5–6 mm long, the basal hairs up to 1 mm long, gland tipped. Style ca. 10 mm long; stigmas 2, apparently globose, ca. 1.2 mm long. Capsule unknown.

This little-known species has been collected at 1100 m elevation and was flowering in June.

PERU. Apurimac, *Weberbauer 5875* (type) (GH, US).

9. Ipomoea teotitlanica McPherson, Contr. Univ. Mich. Herb. 14:85. 1980. TYPE: *H. S. Gentry 22475* (GH, holotype).

"Small trees with gray trunks" (collector's notes). Young stems somewhat ridged on drying, densely tomentose with soft, curly hairs ca. 0.5 mm long; older stems more strongly ridged to much roughened, glabrescent. Leaf blades (immature?) entire, 3–4 cm in diameter with 7–8 lateral veins on each side of the midrib, orbicular, obtuse at the apex, cordate at the base, pubescent above with very slender, more or less appressed hairs 0.3–1.0 mm long, much more densely pubescent beneath (the lower surface completely obscured and appearing lighter in color) with similar hairs, apparently not glandular at the base of the midrib beneath. Petioles 0.8–1.5 cm long, densely tomentose like the stem.

Inflorescences axillary, each cyme consisting of 1 flower, these reduced cymes often borne on shortened tomentose branches up to 5 mm long. Peduncles ca.

0.1 cm long, tomentose. Bracts broadly ovate, 1–1.5 mm long, 1 mm wide, tomentose on the abaxial surface and centrally on the adaxial surface, caducous. Pedicels 1.0–1.5 cm long, stout, tomentose and glabrate, ridged on drying, slightly thickened distally. Sepals 11–16 mm long, 7–10 mm wide, subequal, elliptical to broadly ovate, at least the outer sepals tomentose over the abaxial surface and partially so on the adaxial surface, the curly hairs up to ca. 0.7 mm long. Corolla 5.5–6.5 cm long, ca. 4 cm in diameter, funnelform, glabrous, "light clear yellow" (collector's notes). Stamens 28–38 mm long, the anthers 8 mm long, the basal hairs up to 1 mm long, gland tipped. Style ca. 45 mm long; stigmas 2, globose, ca. 1.5 mm long. Capsule unknown.

The limestone canyon that was the origin of the single specimen of *I. teotitlanica* is indicated in Fig. 2. The specimen was in flower in November.

MEXICO. OAXACA: Tambor, ca. 17 mi. W of San Antonio, District of Teotitlan, *H. S. Gentry 22475* (type) (GH).

10. Ipomoea wolcottiana Rose, Gard. & Forest 7:367. 1894. TYPE: *Palmer 1342* (1891) (US, holotype).

I. calva House, Bot. Gaz. (Crawfordsville) 43:410. *fig. 1.* 1907. TYPE: *Nelson 6992* (US, holotype).

Key to Subspecies

1a. Flowering pedicels 6–17(–19) mm long; Mexico, Central America. .... subsp. *wolcottiana*
1b. Flowering pedicels 23–34 mm long; Peru. .... subsp. *calodendron*

10a. I. wolcottiana Rose subsp. **wolcottiana**

Trees 3–13 m high, the trunk up to ca. 30 cm in diameter. Stems producing a white latex, ridged on drying, usually puberulent when young with hairs up to 0.2 mm long, the branch ends disposed to twining. Leaf blades entire, 6–16 cm long, 3–11 cm wide, with 11–17 lateral veins on each side of the midrib, narrowly to broadly ovate to ovate-lanceolate, acuminate at the apex, truncate or shallowly cordate at the base, the lower surface pubescent with hairs up to 0.3 mm long or merely puberulent on the veins, glabrescent, the upper surface glabrous or occasionally pubescent and glabrescent like the lower surface. Blades biglandular at the base of the midrib beneath with glands 1–2 mm long. Petioles 2–9 cm long, glabrous or pubescent.

Inflorescences terminal or axillary, each cyme consisting of 1 flower, these reduced cymes usually borne on shortened, puberulent branches 2–10 cm long, which sometimes bear reduced leaves. Peduncles 0.1–0.4 cm long, pubescent or glabrous. Bracts 2–6 mm long, 0.5–2.5 mm wide, puberulent and partially glabrescent abaxially, more densely pubescent adaxially, caducous. Flowering pedicels 0.6–1.7(–1.9) cm long; fruiting pedicels 1.6–2.7(–3.0) cm long, usually longitudinally grooved on drying, slightly thickening distally, pubescent. Sepals 6–14(–16) mm long, 5–8(–10) mm wide, subequal or with the outer somewhat smaller than the inner, elliptical, broadly obtuse at the apex (the sides of the sepals only slightly tapering), the abaxial surface puberulent (at least near the base) or short-pubescent (the hairs up to 0.25 mm long), the adaxial surface densely pubescent

with tiny hairs ca. 0.05–0.15 mm long. Corolla 4.5–7 cm long, 6–10 cm in diameter, funnelform, somewhat pubescent near their tips and along their margins, white with deep red in the throat, the interplical regions faintly yellowish. Stamens 12–29 mm long, the anthers 5–7 mm long, the basal hairs ca. 0.5 mm long. Style 18–25 mm long; stigmas 2, globose to cylindrical, 1–3 mm long, 1 mm wide. Capsule 2-locular, 4-valved, the valves 17–22 mm long; seeds 4, long-pilose on the dorsal margins with hairs 10–15 mm long.

Ipomoea wolcottiana subsp. *wolcottiana* inhabits dry, deciduous forests of various densities, including woodlands subject to much grazing. Its distribution is indicated in Fig. 6. It grows at elevations of 50 to 900 m and flowers and fruits between December and March.

MEXICO: JALISCO: Vicinity of Estacion Biologica, UNAM, 3 km SE of Chamela, *McVaugh 26291* (MICH); 9–11 km E of Chamela, *McVaugh 25179* (MICH); 8 miles SW of Pihuamo, *McVaugh & Koelz 1799* (MICH). COLIMA: 15–25 km NW of Santiago, *McVaugh 23019* (MICH); 17–18 km SSW of Colima, *McVaugh 22968* (MICH); between Armería and Colima, *Templeton 9479* (MICH); Manzanillo, 2–18 Mar 1891, *Palmer 1342* (type) (GH, NY, US). MICHOACÁN: 3–6 km SE of San Juan de Lima, *McVaugh 22992* and *22995* (MICH); Coalcomán, *Hinton 16241* (US). GUERRERO: Papanoa, *Langlassé 736* (GH, P, US); La Jurita, *Nelson 6992* (type of *I. calva* House) (US); near Acapulco, Oct 1894–Mar 1895, *Palmer 619* (GH, NY, UC, US). MORELOS: Near Cuernavaca, *Lemmon 210* (MICH). PUEBLA: Near San Luis Tultitlanapa, *Purpus 3532* (MICH). OAXACA: Monte Albán, *Pringle 4965* (MICH). VERA CRUZ: Carrizal, *Goldman 707* (US); 5 miles W of José Cardel, *Fryxell & Bates 848* (US); Mata de Caña, Mpio de Dos Ríos, *Ventura A. 2917* (MICH, NY). TABASCO: Near Plan del Rio, Mpio de Emiliano Zapata, *Gilly, Simpson, & Dodds 72* (MICH). CHIAPAS: Near La Reforma, *Collins & Doyle 42* (US); near Monte Bonito, Mpio of Arriaga, *Ton 3379* (F, MICH); 13 km N of Arriaga, *Breedlove 30632* (DS).

GUATEMALA: Near Chiquimula, *Pittier 1859* (US).

EL SALVADOR: *Renson 228* (US); vicinity of Ciudad Arce, La Libertad, *Allan 7109* (US); Department of Ahuachapán, *Padilla 256* (US); Sonsonate, *Calderon 632* (US); near Acajutla, Sonsonate, *Standley 21941* (US); near Santa Ana, *Standley 19697* (US).

10b. I. wolcottiana Rose subsp. **calodendron** (O'Donell) McPherson, comb. nov.

I. calodendron O'Donell, Lilloa 23:480. 1950. TYPE: *Weberbauer 6396* (US, holotype).

Trees to 10 m high, the trunks up to 30 cm in diameter. Stems producing a white latex, ridged and grooved on drying, finely pubescent with hairs ca. 0.1 mm long, glabrescent. Leaf blades entire, 6–23 cm long, 5.5–14 cm wide, with 10–15 lateral veins on each side of the midrib, ovate, acuminate at the apex, cordate at the base (often deeply so), glabrous above or slightly puberulent near the base, puberulent beneath especially on the midrib and the veins at least when young, glabrescent. Blades biglandular at the base of the midrib beneath with glands 1–2 mm long. Petioles 3–8 cm long, puberulent, glabrescent.

Inflorescence terminal or axillary, each cyme consisting of one flower, these reduced cymes usually borne on shortened, finely pubescent, glabrescent branches. Peduncles 0.2–0.6 cm long, puberulent. Bracts ca. 2.5 mm long, 1.5 mm wide, pubescent on the abaxial surface, caducous. Pedicels 2.3–3.4 cm long, sparsely puberulent, glabrescent. Sepals coriaceous, 8–12 mm long, 5–6 mm wide (the outer about equal to the inner, or slightly smaller), elliptical, obtuse at the apex, finely pubescent and glabrescent abaxially, densely pubescent adaxially with tiny, coarse hairs less than 0.05 mm long. Corolla 5.5–9 cm long, ca. 7 cm in diameter, funnelform, sparsely short-pubescent near the tips of the interplical regions, white

with reddish throat within. Stamens 19–25 mm long (cf. O'Donell's 2.6–3.5 cm), the anthers 7–8 mm long, the basal hairs to ca. 1 mm long, gland tipped. Style described by O'Donell as ca. 26 mm long; stigmas 2, globose. Ovary 2-locular, 4-ovuled. Capsule unknown.

This rarely collected subspecies is known from elevations of 700 to 800 m and flowers between January and July.

Like *I. pauciflora* subsp. *vargasiana,* this taxon is scarcely distinct from its Mexican counterpart. The Peruvian subspecies has, however, several larger ranges in size variation—in leaf length and width, in peduncle and (especially) pedicel length, and in corolla length. Despite this greater variability, the Peruvian plants are so similar to subsp. *wolcottiana* that were it not for their great disjunction, no separate taxonomic rank would be accorded them.

PERU: Valley of the river Quiros, *Weberbauer 6396* (type) (US); Tumbez Valley, *Haught 60* (US); Jalara, *Haught 60a* (US); Cerro Viento, *Haught 201* (US).

SPECIES INQUIRENDAE

Convolvulus arboreus Balb. ex Steudel, Nomencl., ed. 2. 1:407. 1841, nomen nudum. Steudel included this species in *C. arborescens* H.B.K.

C. arboreus Sessé & Moc., Pl. Nov. Hisp. 23. 1888. TYPE: not determined. House referred this species to *I. cuernavacensis,* which is discussed below. The description is inadequate to identify this species. McVaugh (1980) stated that specimens in the Sessé & Mociño herbarium (MA) bearing this name represent both *I. murucoides* and *I. intrapilosa.*

C. quahutzehuatl Sessé & Moc., Pl. Nov. Hisp. 23. 1888. TYPE: not determind. McVaugh (1980) stated that specimens in the Sessé & Mociño herbarium (MA) bearing this name represent *I. murucoides.*

Ipomoea cuernavacensis House, Bot. Gaz. (Crawfordsville) 43:410. 1907. TYPE: *Rose & Painter 6963* (US, holotype), not *Rose & Painter 6863,* as stated in House (1908). *Ipomoea cuernavacensis* is probably a synonym of *I. aborescens* because, although the leaf base of the type material of the former resembles that of *I. murucoides* in being truncate, in details of the stem and leaf pubescence it strongly resembles *I. arborescens.* It is completely sterile, and therefore some doubt must remain about its identity. Since no other similar specimens have been seen, I suspect that it came from a somewhat unusual individual of *I. arborescens.*

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CHROMOSOME CYTOLOGY OF BRUNIACEAE[1]

PETER GOLDBLATT[2]

ABSTRACT

The chromosome numbers are reported for twenty-one species in eight genera of Bruniaceae, a small family almost entirely restricted to the Cape Floristic Region of South Africa, an area with a very distinctive flora. With the only previous count in the family disregarded, a base number of x = 11 is suggested as fundamental in the family. A diploid number of $2n$ = 22 is recorded in the monotypic and apparently primitive *Audouinia*. Other genera counted evidently have a base number in the x = 20–23 range and thus may be palaeopolyploid in comparison to *Audouinia*. *Staavia*, *Raspalia* and *Lonchostoma* have x = 22, with the widespread *S. radiata* tetraploid, $2n$ = ca. 88. Exact base numbers in the remaining genera examined are uncertain owing to difficulties in counting: *Pseudobaekia* has n = ca. 22; *Nebelia* n = 22 and ca. 23; *Brunia* n = ca. 20 and 23; and *Berzelia* n = 20 and ca. 21. *Berzelia ecklonii* and *B. abrotanoides* are tetraploid, n = 80–88, while *B. intermedia* has diploid, tetraploid and hexaploid races.

INTRODUCTION

The Bruniaceae is a small family of twelve genera and between seventy and eighty species, endemic in South Africa. All but a few species occur only in the Cape Floristic Region in the extreme southwestern part of the Cape Province, an area of predominantly mediterranean climate. The family consists of medium to small sized shrubs, almost all with sclerophyllous ericoid leaves, and it forms a very characteristic element of the flora. This survey of the cytology of the family was undertaken in collaboration with Mrs. E. Powrie, who began a systematic revision of the family some ten years ago, a study cut short by her recent death. Our initial hope, that cytological data would provide data of help in determining generic and family relationships, has not been realized; however, the information obtained so far seems worth publishing for itself, and it may be of use to others in the future.

MATERIALS AND METHODS

Chromosome studies were made from both mitotic and meiotic material. Mitotic chromosome counts were obtained from root tips of seedlings cultivated by Powrie in South Africa, and at the Missouri Botanical Garden. All seed was collected in the wild. Both paraffin section (Goldblatt, 1971) and squash techniques (Goldblatt, 1976, 1979) were employed. In the latter case root tips were pretreated in 0.1% aqueous colchicine or in hydroxyquinoline solution, both stored overnight at refrigerator temperature, before fixing. After acid hydrolysis, root tips were stained in lacto-propionic orcein.

Meiotic counts were made from anther squashes, all flower buds being collected wild. Vouchers are deposited at the Bolus Herbarium (BOL), University

[1] I thank Dr. S. Carlquist and the late Mrs. E. Powrie for seed of the species used in this study; and Miss E. Esterhuysen for her guidance in the field in searching for rare species, as well as for seed samples.

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of Cape Town, South Africa, Missouri Botanical Garden (MO), St. Louis, Missouri or at Rancho Santa Ana Botanical Garden (RSA), California.

Results

The putatively primitive (Pillans, 1947) monotypic *Audouinia* has $n = 11$ (Table 1), making it the only genus of the eight counted with a chromosome number at the palaeodiploid level.

Two species of *Lonchostoma* counted, one of *Pseudobaekia*, two of *Raspalia* and three of *Staavia*, have $n = 22$ or ca. 22, while the only common and widespread species of *Staavia*, *S. radiata* is tetraploid, $2n =$ ca. 88.

Species of *Nebelia* and the closely allied *Brunia* are, like the previous genera, basically tetraploid, with haploid numbers in the range $n = 20, 22, 23$. I have obtained counts of $2n = 40$ or ca. 40 in *Brunia albiflora* and *B. stokoei* but $2n = 46$ in *B. nodiflora*. Counts in *Nebelia* are $2n =$ ca. 44 for *N. paleacea* and *N. fragarioides*, while *N. stokoei* has $2n =$ ca. 46.

In the apparently most advanced genus *Berzelia*, most species have $n = 20$ (ca. 20, ca. 21) but *B. ecklonii* and *B. abrotanoides* are neotetraploid, $n =$ ca. 40, while *B. intermedia*, the most widespread species of the genus, has races with $n =$ ca. 20, ca. 80–86, and ca. 120.

Chromosomes of all species examined are similar and uniformly small, ranging in size at mitotic metaphase from 1.5–2.5 μm. Small size combined with high number has made it difficult to obtain accurate counts in several species.

The only previous count in Bruniaceae apart from a summary of present results given by Raven (1975), is a record of $n =$ ca. 8 (Saxton, 1970) in *Staavia glutinosa* obtained incidentally in the course of an embryological study. This report is almost certainly incorrect.

Discussion

The most striking observation resulting from this study is the sharp difference in basic ploidy level between *Audouinia* and the seven other genera examined. *Audouinia* is apparently the most primitive genus of Bruniaceae, a relict of very limited distribution, and the only genus with a trilocular ovary. It is the only diploid encountered in this study, thus standing in isolation cytologically from base numbers of $x = 20–23$ in the other genera studied.

Most closely allied to *Audouinia*, of those genera examined, are *Pseudobaekia* and *Lonchostoma*, which also have axillary inflorescences, but a bilocular (–unilocular) ovary. *Lonchostoma* and *Pseudobaekia* as well as *Staavia* and *Raspalia* (capitate inflorescences) have $x = 22$.

Nebelia and *Brunia* are closely related (Powrie, pers. comm.), perhaps not generically separable, and these, together with *Berzelia* form a distinctive group of Bruniaceae, seemingly well separated from the other genera. All have globose, capitate inflorescences. *Brunia* (bilocular to unilocular ovaries) and *Nebelia* (unilocular ovaries) have dehiscent fruits (according to Pillans, 1947), while *Berzelia*, also with unilocular ovaries, have indehiscent fruits. These genera are also tetraploid in comparison with *Audouinia*, but unfortunately, owing to difficulties in making accurate counts, the exact base number has not been determined. I am

TABLE 1. Chromosome numbers in Bruniaceae—All localities are in the Cape Province, South Africa.

Species	Chromosome Number *n*	Chromosome Number 2*n*	Collection Data
Audouinia			
A. capitata (L.) Brongn.	11		Cape Point Reserve, *Goldblatt 1844* (MO)
		22	Karbonkelberg, Cape Peninsula, *Powrie 255* (BOL)
Lonchostoma			
L. purpureum Pill.	22		Somerset Sneeukop, *Goldblatt 1646* (MO)
L. monogynum (Vahl.) Pill.	22		DuToit's Kloof Mts., *Goldblatt 2071* (MO)
		ca. 44	Buffelshoek, Ceres, *Esterhuysen 32676* (BOL)
Pseudobaekia			
P. africana (Bwm. f.) Pillans		ca. 44	Vogelgat, Hermanus, *Goldblatt 5345* (MO)
Staavia			
S. capitella (Thunb.) Sond.	22–23		Silverstream, Villiersdorp, *Goldblatt 1813* (MO)
S. zeyheri Sond.	22–23		Near Riviersonderend, *Goldblatt 2061* (MO)
S. doddii H. Bolus		ca. 44	Cape Point Reserve, *Goldblatt 1845* (MO)
S. radiata (L.) Dahl.		ca. 88	Cape Point Reserve, *Powrie s.n.* no voucher
		ca. 88	Sandveld near Darling, *Powrie s.n.* no voucher
Raspalia			
R. globosa (Lam.) Pillans		ca. 44	Nuweberg Reserve, *Powrie 42* (BOL)
R. microphylla (Thunb.) Brongn.	ca. 22		Rooi Els, *Powrie s.n.* no voucher
Nebelia			
N. fragarioides (Willd.) O. Kuntze		ca. 44	Rooi Els, *Powrie s.n.* no voucher
N. paleacea (Berg.) Sweet	ca. 22		Rooi Els, *Carlquist 4780* (RSA)
N. stokoei Pillans		ca. 46	Hex R. Mts., W. Milner Peak *Carlquist 5022* (RSA)
Brunia			
B. albiflora Phill.		40	Stalberg, Rooi Els, *Powrie s.n.* no voucher
		ca. 40	Vogelgat, Hermanus, *Carlquist 4535* (RSA)
B. nodiflora L.		46	Cape Prov., *Carlquist 4608* (RSA)
B. stokoei Phill.		ca. 40	Rooi Els, *Powrie s.n.* no voucher
Berzelia			
B. abrotanoides (L.) Brongn.		ca. 80	Vyeboom, *Powrie 148* (BOL)
		ca. 80	Cape Point Reserve, *Powrie s.n.* no voucher
var. *pilosa* (L.) Brongn.		ca. 80	Kraaifontein, *Powrie 127* (BOL)
B. burchellii Dummer		40	Garcias Pass, *Powrie 151* (BOL)
B. ecklonii Pillans		ca. 80–86	Rooi Els, *Carlquist 4965* (RSA)
B. galpinii Pillans		40	Garcias Pass, *Carlquist 4541* (RSA)
		ca. 40	Garcias Pass, *Powrie 153* (BOL)
		ca. 40	Near Muisrkaal, Grootwaterval, *Powrie s.n.* no voucher
B. intermedia Schldl.		ca. 42	Natures Valley, *Powrie s.n.* no voucher
		42	Garcias Pass, *Carlquist 4742* (RSA)
		ca. 80–86	Swellendam, *Powrie s.n.* no voucher
		ca. 80–86	Albertinia, *Powrie 254* (BOL)
		ca. 80–86	Robinsons Pass, *Powrie s.n.* no voucher

TABLE 1. Continued.

Species	Chromosome Number *n*	Chromosome Number *2n*	Collection Data
		ca. 120	Arrieskrall, Palmiet River Valley, *Powrie s.n.* no voucher
B. lanuginosa (L.) Brongn.		40	Stalberg, Rooi Els, *Powrie s.n.* no voucher
B. rubra (Willd.) Schldl.		ca. 40	Maanskyn Kop, Hermanus, *Powrie 244* (BOL)

therefore uncertain whether the apparent diversity of numbers in *Brunia* and *Berzelia* is correct. The count of $n = 22$ in *Nebelia* seems reasonable in view of the same number having been recorded in four other genera and $n =$ ca. 23 in *N. stokoei* may be incorrect or due to the presence of supernumeraries. The counts of $n = 20$ and ca. 20 in *Brunia* were obtained after long, careful observation and I had no reason at the time to doubt them. However, my count of $n = 23$ in my material of *B. nodiflora* is almost certainly correct but whether due to supernumeraries cannot yet be determined.

Berzelia from my observations almost certainly has $x = 20$, although some higher counts were made in *B. intermedia*, $n =$ ca. 21. Interestingly, in this most specialized genus, there are cases of neopolyploidy. Four of the species examined are diploid, two tetraploid, and one, *B. intermedia*, has diploid, tetraploid and hexaploid forms. In this widespread species, eastern populations are tetraploid, the most western population counted is hexaploid, while the two diploids were collected in about the middle of the range.

In summary, the pattern suggested from the available information is the following. Bruniaceae may have a basic number for the family of $x = 11$. *Audouinia* stands out as an isolated diploid relict compared with the other genera, all tetraploid on the base $x = 11$ or 10. Exact counts were not obtained in *Brunia* and *Nebelia*, which may have $n = 20$ and 23, and $n = 22$ and 23 respectively. It suggests that the diploid progenitors of this group had $x = 10$, 11 and possibly 12. *Berzelia*, the most specialized genus, most likely has $x = 20$, suggesting aneuploidy from the family base, to $x = 10$ and subsequent polyploidy. Neopolyploidy in the family is restricted to four species of the twenty-two counted, 18%, with one of the polyploids having diploid, tetraploid and hexaploid races.

RELATIONSHIPS

The immediate relationships of Bruniaceae are obscure. The family is usually considered to have broadly Rosalean affinities. Modern phylogenetic treatments vary somewhat but Bruniaceae are generally regarded as one of several unspecialized but not especially primitive families considered to be Rosalean in a broad sense. Taktadjan (1969) and Cronquist (1968) place the family in Rosales while Thorne (1968) assigns it to Rosiflorae-Pittosporales, an order of markedly southern distribution. The treatment by Dahlgren (1975) differs in placing Bruniaceae in Hamamelidanae–Cunoniales. A flavonoid study by Jay (1968) points to the family having an isolated position in Rosales; Bruniaceae markedly lack ellagic

acid, characteristic of Hamamelidaceae and Saxifragaceae. A recent study by Carlquist (1978) of wood anatomy supports the traditional placement of the family. However, Carlquist points particularly to relationships, based in wood anatomy, with the Cape endemics Geissolomataceae and Grubbiaceae, families included by Thorne in his Pittosporales.

These families are unfortunately unknown cytologically, and Rosales are cytologically diverse, so that cytology seems unlikely to be of value in determining relationships of Bruniaceae.

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CHROMOSOME NUMBERS IN LEGUMES II[1]

PETER GOLDBLATT[2]

ABSTRACT

Original chromosome counts are presented for 95 species in 78 genera of Leguminosae. Of these, 50 are first reports for genera, and 71 are first reports for species. The evolutionary or systematic significance of much of the data has been discussed in a separate paper (Goldblatt, 1981), and this article serves mainly for full documentation of the counts. New information, not previously dealt with, concerns *Myroxylon* (Papilionoideae–Sophoreae). The genus was previously reported as n = 14, but material I have studied clearly has $2n$ = 26, which is compatible with the number of n = 13 in the related genus *Myrospermum*.

INTRODUCTION

Counts presented here are largely the first reports for genera, or first counts for species in genera where the cytological record was confusing or seemed particularly interesting. As mentioned in a previous paper (Goldblatt & Davidse, 1977) this project was undertaken in preparation for the Conference on Leguminosae held at Kew, London in 1978. Since the Leguminosae are a very large family, it was impractical to attempt chromosome study of all species available, or even all uncounted species. Instead I have concentrated on filling gaps in the cytological record at generic level, or have examined species of certain genera where the existing record seemed confused or particularly interesting and thus worth further attention.

Almost all of the new generic records presented here have been mentioned in the paper (Goldblatt, 1981) presented at the Leguminosae Conference and this article serves to fully document these counts. This being the case there is no purpose in discussing the data here. A few counts made after publication of my review of cytology of Leguminosae are discussed briefly, notably that for *Myroxylon*. Methods employed with root tips were as described in several previous papers (Goldblatt, 1976; Goldblatt & Gentry, 1979) and involved hydroxyquinoline pretreatment, and squashing in lacto-propionic orcein. Data are presented in tabular form (Table 1). Genera arranged in subfamilies and tribes according to the classification system adopted in the published proceedings of the Leguminosae Conference (Polhill & Raven, 1981).

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TABLE 1. Chromosome numbers of Leguminosae. Entries preceded by one asterisk (*) are the first report for that species; entries with two asterisks (**) are the first report for that genus. Genera are arranged in tribes following the treatments in Polhill & Raven (1981).

Species	Chromosome Number *n*	Chromosome Number 2*n*	Collection and Voucher Data
		MIMOSOIDEAE	
		Mimoseae	
***Dinizia excelsa* Ducke		26 (–28)	Brazil, Manaus Exp. Station, km 60, *DaSilva 295* (INPA).
Schrankia leptocarpa DC.		52	Brazil, Belem, Para, *Pires 75130* (MO)
S. uncinata Willd.		26	U.S.A., Nebraska; exact locality unknown; cult. MBG, *Goldblatt 4664* (MO).
		Adenanthereae	
***Gagnebina pterocarpa* (Lam.) Baill.		26	Mauritius, Quatre Bornes, *Lorence 2651* (MO).
**G. sp.		26	Comoro Is., Mayotte, *Lorence 2846* (MO).
***Goldmania foetida* (Jacq.) Standl.		26	Mexico, Sinaloa, *Gentry, Barclay & Arguelles 19450* (US).
***Parapiptadenia rigida* (Benth.) Brenan		26	Argentina, orig. loc. unknown, seed ex Jard. Bot. Carlos Thuys; cult. MBG, *Goldblatt 4652* (MO).
		Ingeae	
Calliandra surinamensis Benth.		16	Cult., Raya Bogor, origin unknown, cult. MBG, *Goldblatt 5480* (MO).
C. magdalenae (Bert.) Benth.		16	Cult., Summit Gardens, Panama, origin unknown, *Mori & Kalunki 5089* (MO).
**C. confusa* Sprague & Riley		22	Costa Rica, Alajuela, Finca Los Ensayos, *Barquero s.n.* (MO).
***Serianthes kanehirae* Fosberg		26	Caroline Is., Korror Is., old temple grounds, cf., *Fosberg 26770* (US).
***Wallaceodendron celebicum* Koorders		26	Locality unknown, ex Wahaiwa Bot. Garden, Hawaii, *Anon. s.n.* (MO).
		CAESALPINIOIDEAE	
		Caesalpinieae	
***Pterolobium stellatum* (Forsk.) Brenan		24 (–26)	Kenya, Nairobi, Dagoretti, corner near bridge, *Gachathi 180B* (EA).
***Sclerolobium* sp.		26	Brazil, orig. loc. unknown, cult. Jard. Bot. Rio de Janeiro, *de Lima 1082* (US).
Peltophorum cf. *ferrugineum* Benth.		26	Cult. Jard. Bot. Facultad Agronomia U.C.V. Maracay, Venezuela, orig. loc. unknown, *Berry & Plowman 3384* (MO).
***Storkiella* sp. indet.		26	New Caledonia, *McPherson 2128* (MO).
		Cassieae	
Apuleia leiocarpa (Vogel) MacBride		28	Brazil, loc. unknown, cult. MBG, *Goldblatt 4665* (MO).
Ceratonia siliqua L.		24	Israel, *Goldblatt 5014* (MO).
		Cercideae	
***Adenolobus pechuelii* (Kuntze) Torre & Hillc.		28	Namibia, near Walvis Bay, *Seely s.n.* no voucher.
Bauhinia (*Lysiphyllum*) *hookeri* (F. Muell.) Pedley		26	Cult., Brisbane, Australia, origin unknown, *Pedley A7771* (BRI, MO).
**Bauhinia* (*Gigasiphon*) *macrosiphon* Harms		26	Kenya, Coast, Mua hills, *Gachathi s.n.* no voucher.

TABLE 1. Continued.

Species	Chromosome Number n	Chromosome Number 2n	Collection and Voucher Data
**Bauhinia (Barklya) syringifolia* (F. Muell.) Wunderlin		26	Cult. Botanic Gardens, Brisbane, Australia, origin unknown, *Pedley A1772* (BRI, MO).
		Detarieae	
Colophospermum mopane Kirk.		34 (–36)	S. Africa, Transvaal, Letaba Rest Camp, cult. MBG, *Goldblatt 4663*.
***Daniella oliveri* Hutch. & Dalz.		22	Ghana, loc. unknown, coll. A. Enti, cult. MBG, *Goldblatt 4662* (MO).
		Amhersteae	
***Brachystegia spiciformis* Benth.		24	Rhodesia, Salisbury, native plants in Botanic Garden, cult. MBG, *Goldblatt 4661* (MO).
		PAPILIONOIDEAE	
		Swartzieae	
**Swartzia laevicarpa* Amshoff		~28	Brazil, Amazonas, Rio Negro, *Monteiro & Coêlho 1369* (INPA 63866).
		Sophoreae	
***Cadia purpurea* (Picc.) Ait.		18	Kenya, cult. University of Nairobi, Chiromo, *Gachathi 184* (EA).
Cladrastis lutea (Michx.) K. Koch		28	Cult. MBG. origin unknown, *Lorence et al. 309* (MO).
Myroxylon balsamiferum (L.) Harms		26	Peru, Loreto, *Gentry 29117* (MO).
***Myrospermum frutescens* Jacq.		26	Nicaragua, Chontales Dept., *Stevens 6456* (MO).
Sophora japonica L.		28	Cult. MBG, origin unknown, *Goldblatt 4987* (MO).
**S. affinis* Torr.		28	U.S.A., Texas, Real Co., *Poole s.n.* (MO).
		28	U.S.A., Oklahoma, *Estes s.n.* (MO).
**S. (Echinosophora) koreensis* Nakai		22	Cult. MBG, orig. loc. not known, ex Tokyo Bot. Gard., *Goldblatt 4986*.
**S. arizonica* Watson		18	Mexico, Chihuahua, cult. MBG, *Goldblatt 5091* (MO).
***Ammothamnus lehmannii* Bunge		18	Cult. MBG, orig. loc. unknown, ex Hort. Bot. Princip. Acad. Sci. USSR, Moscow (no voucher).
***Ammodendron conollyi* Bunge ex Boiss.		18	U.S.S.R., Turkmenistan ex hort. Ashkabad, cult. MBG, *Goldblatt 4657* (MO).
**Maackia chinensis* Takeda		18	Cult. MBG, orig. source unknown, *Goldblatt 4676* (MO).
**Pericopsis (Afrormosia) angolensis* (Baker) Van Meeuwen		18	Malawi, Mzuzu, *Pawek 8241* (MO).
		Dalbergieae	
***Xeroderris stuhlmanii* (Taub.) Mendonca & Sousa		24	Rhodesia, exact locality unknown, cult. MBG, *Goldblatt 5481* (MO).
Dahlergia sissoo Roxb.		20	Cult. Israel, Ein Gedi, *Goldblatt s.n.* (MO).
***Cyclolobium vecchii* A. Samp.		18	Brazil, Sao Paulo, Moji Gaussu Reserva Florestal, *Handro 879* (SP).
Geoffraea decorticans (Gill. ex Hook. & Arn.) Burk.		20	Chile, Prov. Antofagasta, San Pedro de Atacama, *Zöllner s.n.*, no voucher.

TABLE 1. Continued.

Species	Chromosome Number *n*	Chromosome Number 2*n*	Collection and Voucher Data
Platymiscium cf. *polystachyum* Benth. ex Seem.		20	Colombia, Dept. Cundinamarca, near Puerto Bogota, *Gentry 18115* (MO).
	Tephrosieae		
***Willardia mexicana* (Wats.) Rose		22	Mexico, Sonora, *Gentry s.n.* (no voucher); cult. MBG, *Goldblatt 4654* (MO).
***Kunstleria blackii* (F. Muell.) Polhill		22	Australia, Queensland, Brisbane, *Pedley 5005* (K, L, MO).
***Barbieria pinnata* DC.		20	Peru, Amazonas, *Schunke 8307* (MO).
	Galegeae		
***Smirnovia turkestanica* Bunge		16	Iran, Kashan, Shuzeyd-ahad, *Moussain & Tehrani s.n.* (EVIN-30708E).
	Robinieae		
***Peteria scoparia* Gray	10		U.S.A., New Mexico, San Juan Co., *Spellenberg 4873* (MO).
***Corynella pauciflora* DC.		20	Puerto Rico, Guiniquila, *Woodbury s.n.*, no voucher.
Glottidium vesicarium (Jacq.) Harper		12	Orig. locality not known, seed ex U.S.D.A. Plant Introd. Station, Savanna, Georgia, cult. MBG, *Goldblatt 4625A* (MO).
	Aeschynomeneae		
***Pictetia aculeata* (Vahl) Urban		20	Puerto Rico, *Raven 26620* (MO).
**Kotschya uguenensis* (Taub.) F. White		28	Malawi, Northern Province, *Pawek 10063* (MO).
***Amicia zygomeris* DC.		38	Mexico, Chihuahua-Durango, 42 mi W of Parral, *Gentry, Correll & Arguelles 17934* (US, LL).
***Chapmannia floridana* Torr. & Gray		22	U.S.A., Florida, Osceola Co., *Wunderlin & Shuey 5766* (MO).
	Desmodieae		
***Christia vespertilionis* (L.) Bak. f.		22	Seed from Bot. Gard. München, origin unknown, cult. MBG, *Goldblatt 4658* (MO).
Phyllodium pulchellum Desv.		22	Hong Kong, exact locality unknown, seed ex Department of Agriculture & Fisheries, cult. MBG, *Goldblatt 4660* (MO).
Desmodium (*Hanslia*) *ormocarpoides* DC.		22	New Guinea, Papua, Sankwap logging area, *Lae* (no voucher).
	Psoraleae		
**Psoralea frutescens* (L.) Druce		22	South Africa, Cape, C. Peninsula, *Goldblatt 5544* (MO).
	Phaseoleae–Erythrininae		
**Erythrina decora* Harms		42	Namibia, Okaukuejo dist., farm Otjitambi, *Geiss 13603* (WIND).
**E. merrilliana* Kruk.		42	New Guinea, Papua, Bulolo, *Galore s.n.* (MO).
**E. megistophylla* Diels		42	Ecuador, Rio Palenque, *Dodson s.n.* in 1978 (MO).
**E. acanthocarpa* E. Mey.	42		S. Africa, original locality unknown, cult. plant in Oudtshoorn, Cape, *Goldblatt 2966* (MO).

TABLE 1. Continued.

Species	Chromosome Number *n*	Chromosome Number 2*n*	Collection and Voucher Data
		Phaseoleae–Kennediinae	
***Vandasia retusa* (Benth.) Domin.		22	Australia, Queensland near Mossman, *Stables 2329* (BRI).
		Phaseoleae–Glycininae	
***Nogra grahamii* (Benth.) Merrill		22	India, Jashpur M.P., *Tiwari s.n.* (no voucher).
***Eminia antennulifera* Taub.		22	Malawi, Rumphi district, *Pawek 8866* (MO).
***Neorautanenia mitis* (A. Rich.) Verdc.		22	Malawi, Karonga-Chitipa, *Pawek s.n.*, no voucher, cult. MBG, *Goldblatt 4655* (MO).
***Pseudovigna argentea* (Willd.) Verdc.		22	Tanzania, University of Dar es Salaam Campus, *Wingfield s.n.* (no voucher).
		Phaseoleae–Phaseolinae	
Dipogon lignosus (L.) Verdc.		22	S. Africa, Cape, Cape Peninsula, *Esterhuysen s.n.* (no voucher).
		Phaseoleae–Diocleinae	
Pachyrrhizus erosus (L.) Urban		22	Rep. Dominica, Rio Arriba, *Jimenez 8697* (MO).
***Oxyrhynchus volubilis* Brandeg.		24	Bahama Islands, New Providence, *Correll 48408* (MO).
		Phaseoleae–Cajaninae	
***Bolusafra bituminosa* (L.) Kuntze		22	S. Africa, Cape, Kalk Bay Mt., *Goldblatt 1526* (MO).
		Trifolieae	
***Factorovskya aschersoniana* Eig		14	Israel, exact locality unknown, cult. MBG, *Goldblatt 4656* (MO).
		Coronilleae	
Securigera securidaca (L.) Degen. & Doerfl.		12	Turkey, between Ahlat and Karahasan, *Osman Tosun 1403* (Herb. Agrorum Turcicum, Ankara).
***Antopetitia abyssinica* A. Rich.		14	Malawi, Vipya Mts. cf. *Pawek 6733* (MO).
		Hedysareae	
***Eversmannia subspinosa* (Fisch.) B. Fedtsch.		16	ex Hort. Bot. Acad. Sci. Uz. SSR, Tashkent, original loc. unknown, cult. MBG, *Goldblatt 4653* (MO).
***Taverniera numullaria* DC.		16	Pakistan, Masriot, near Rawalpindi, cult. MBG, *Goldblatt 4653* (MO).
		Bossiaeeae	
***Ptychosema trifoliatum* F. Muell.		18	Western Australia, 12 mi N of Cue, *Demarz 5679* (PERTH).
***Lamprolobium fruticosum* Benth.		18	Queensland, Hales Siding, W of Herberton, *Jackes s.n.* (MO).
***Muelleranthus stipularis* (Black) Lee		18	N. Territory, Hamilton Downes Stn., *Nelson 2442* (NT).
		Podalyrieae	
***Cyclopia maculata* (Andr.) Kies		36	S. Africa, Cape, exact locality not known, ex hort. Kirstenbosch, *Henderson 2130* (NBG).

Table 1. Continued.

Species	Chromosome Number *n*	Chromosome Number 2*n*	Collection and Voucher Data
Virgilia oroboides (Berg.) Salter		54	S. Africa, Cape, Hermanus, Fernkloof, *Goldblatt 5174* (MO).
		Liparieae	
***Liparia splendens* (Burm. f.) Bos & de Wit ssp. *splendens*		18	S. Africa, Cape, Trolley Track, Kirstenbosch, *Compton 10320* (NBG).
***Hypocalyptus sophoroides* (Berg.) Baill.		20	S. Africa, Cape, Worcester distr., *Esterhuysen s.n.* (no voucher).
***H. coluteoides* (Lam.) R. Dahlgr.		20	S. Africa, Cape, Garcias Pass., *Goldblatt 4898* (MO).
***H. oxalidifolius* (Baill.) Phill.		20 + 1–2B	S. Africa, Cape, Near Hermanus, *Goldblatt 4787* (MO).
		Crotalarieae	
**Rafnia triflora* Thunb.		16	S. Africa, Cape, Kalk Bay Mt., *Goldblatt 5101* (MO).
**R. amplexicaulis* Thunb.		16	S. Africa, Cape, mts. W of Trawal, *Goldblatt 4026* (MO).
Lotononis serpens (E. Mey.) R. Dahlgr.		18	S. Africa, Cape, Nieuwoudtville, *Goldblatt 3970* (MO).
**Lotonis platycarpos* (Viv.) Pic. Serm. var. *abyssinica* (Hochst. ex A. Rich.) Pic. Serm.		18	Namibia, Otjimbingwe, *Geiss 10468* (MO).
***Dichilus lebeckioides* DC.		28	S. Africa, Transvaal, Silverton, *Nel 261* (PRE).
D. sp. indet.		28	Zimbabwe (Rhodesia), *Corby 1189* (SRGH).
***Anarthrophyllum andicola* (Gil.) Reiche		24	Chile, Prov. Colchagua, *Zöllner 9180* (MO).
***A. elegans* Phil. f.		24	Chile, Prov. Santiago, San Gabriel, *Schlegel s.n.* (no voucher).
		Thermopsideae	
Pickeringia montana Nutt.		28	U.S.A., California, San Diego Co., *Zedler s.n.* (MO).
***Ammopiptanthus nanus* (Popov) S.H.		20	Orig. local. unknown, ex Hort. Bot. Acad. Sci. Uzbek R.S.S., cult. MBG, *Goldblatt 4985* (MO).
		Genisteae	
***Gonocytisus angulatus* (L.) Spach		50	Turkey, Izmir, Banova-Manisa roadsides, *Osman Tosun 1148* (Herb. Agrorum Turcicum, Ankara).

Discussion

Two counts were made too late for inclusion in my review paper (Goldblatt, 1981) on cytology of Leguminosae. The first is a second report of $2n = 28$ in *Dichilus*, which further supports the record of polyploidy in this genus, *D. lebeckioides*, the only other species counted, also having $2n = 28$.

The other concerns the small, possibly ditypic Neotropical genus *Myroxylon* of the tribe Sophoreae. Atchison (1951) previously reported $2n = 28$ in *M. pe-*

reirae, a synonym of *M. balsamiferum*, and the same species I counted. Moreover her illustration of the count clearly shows $2n = 18$. Quite clearly the material I counted, the identity of which is not in doubt, has $2n = 26$. Atchison's count must be regarded as erroneous, possibly due to misidentification of the plants studied. The closest relative of *Myroxylon* is *Myrospermum*, also $n = 13$ and these appear to constitute a natural grouping within Sophoreae. The report here of $n = 13$ in *Myroxylon* substantiates the belief that they are related.

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A NOTE ON THE REDISCOVERY OF *ARGYROLOBIUM INVOLUCRATUM* (THUNB.) HARV. AND THE GENERIC BORDERLINE BETWEEN *ARGYROLOBIUM* AND *MELOLOBIUM* (FABACEAE–CROTALARIEAE)[1]

ROLF DAHLGREN[2] AND PETER GOLDBLATT[3]

ABSTRACT

The species currently known as *Argyrolobium involucratum,* and previously known only from the type collection made by Carl Thunberg in the 1770s, has been rediscovered on the Roggeveld escarpment, Cape Province, South Africa. Until now the distribution of the species has been unknown because this information was not given in Thunberg's (1800) protologue of *Psoralea involucratum,* the basionym. The species has many attributes unusual in *Argyrolobium,* but characteristic of the related Crotarioid genus *Melolobium,* and we suggest that this species may correctly belong in the latter genus.

A species which has been identified as *Argyrolobium involucratum* (Thunb.) Harv. was collected in 1976 by Goldblatt in the Williston district of the Cape Province, South Africa. It was located 68–70 km south of Calvinia on the Blomfontein road to Middelpos and was found growing in clay soil among rocks at an altitude of ca. 1300 m. This area lies along the edge of the Roggeveld escarpment and it receives considerably more precipitation than the country lying immediately east, towards the interior.

The find is of great interest because the distribution of this species was not previously known. No locality was given in the protologue of *Psoralea involucrata* Thunb., the basionym of the species, and since then the species does not seem to have been collected.

We surmise that Thunberg collected his specimens in the same general area, if not at the same site on his third trip into the interior of the Cape, to the Roggeveld, in 1774 (Karsten, 1939). While the exact route Thunberg took on this journey seems to be unknown, Karsten indicates he travelled south from the Hantam Mts. (Calvinia) along the foot of the Roggeveld escarpment, but at some point ascended the 800 m range onto the plateau, and here he probably made his type collection of *Psoralea involucrata.*

The population of *Argyrolobium involucratum* was fairly localized, as far as was possible to estimate, and grew along the road on a rocky ridge about 0.5 km from the escarpment edge. Most likely there are more populations along the escarpment in inaccessible sites, but no plants were seen elsewhere although the species is conspicuous and the road traverses the escarpment for some distance before turning inland towards Middelpos. A formal account of the species is as follows.

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Argyrolobium involucratum (Thunb.) Harv., Flora Cap. 6:75. 1862.—(Fig. 1.)

Psoralea involucrata Thunb., Prod. Pl. Cap. 2:136, 1800; Fl. Cap. 2:607, 1823. TYPE: South Africa, Cape "e Cap. b. Spei. Thunberg *Psoralea involucrata,*" *Thunberg s.n.* (UPS–THUNB 17575, lectotype).

Erect or ascending shrub 50–100 cm high, with rigid, densely and shortly villous branches. Leaves glabrous (except on the petiole), pale light-green, trifoliolate, shortly petiolate, with large stipules that are connate, perfoliate, and adnate to the petiole. Stipules of most vegetative leaves ovate, between 3 × 5 and 5 × 7 mm, those in lateral short shoots smaller, but those of the upper leaves ovate to broadly ovate, often pale on the lower parts and up to 11 × 8 mm, fused on the leaf-opposed side for up to 3–4 mm. Petiole (free part) 0.2–1.0 mm long, villous. Leaflets obovate, conduplicate, 2–5 × 1.5–3 mm, rounded to acute, with a distinct acute-apiculate point.

Inflorescence a pseudo-umbel of, as a rule, 4–6 flowers; the pedicels and often the base of the calyces enclosed by the sheathlike stipular involucre of the uppermost leaf. The internode below this leaf may be longer than the others and slightly peduncle-like. Pedicel 3–4 mm long in flowering, up to 9 mm in fruiting stage, villous, merging gradually into the calyx. Bract and bracteoles lacking. Calyx cylindrical (–campanulate), 2.5–9.5 mm long incl. lobes, pale yellowish on basal part, more or less deeply purplish on lobes and distal parts of tube, sparsely pubescent on the tube, more densely so on the lobes. Upper two lobes triangular, ca. 3.2 mm long and almost equally broad at base; lower three lobes mutually coherent to a lip, narrower and shorter than the upper, the lowest about 2 × 1 mm or less (Fig. 1C). Corolla pale yellow with purplish tinge especially on back of vexillum and distal parts of alae, becoming increasingly purple when fading. Standard blade ovate, obtuse, ca. 7.5–8.5 × 6 mm large, glabrous except along the midrib of the back; claw ca. 4 mm. Wing blades linear-elliptic, ca. 7.5–8.5 × 3.7–4.0 mm, rounded at the apex and with a rounded upper basal lobe, subglabrous but with a line of few hairs on the apical half of the outer side; basal upper part with ca. 5–7 rows of small lunulate foldlets; claws ca. 5.0–5.5 mm long. Keel blades lunate, 7.0–7.8 × 3.5–4.0 mm, with slightly concave upper margin, obtuse at apex, with a slight lobe at the base of the upper side, apical half pubescent, a low longitudinal pouch present on basal half; claws 5–5.5 mm long. Stamens united to form a sheath with a slit going right to the base on either side of the upper medial stamen; filaments fused for ca. 15–20 percent of their length. Anthers alternately long (1.0–1.2 mm) and basifixed, and short (ca. 0.8 mm) and dorsifixed. Pistil sessile (stipeless), the ovary linear, densely pubescent, merging into the upcurved style which is likewise densely pubescent except on the apical upcurved parts comprising ca. 3 mm of the length. Stigma small, apical, capitate. Ovules mostly 6–7 in number. Legume (Fig. 1I) linear, ca. 30 × 35 mm large, very slightly curved, covered with dense villous pubescence, supplemented with short glandular hairs (Fig. 1J). Seeds (causing 5–7 prominent convexities on legume surface), ca. 2.6 × 1.8 mm, smooth, dark and dull in color.

Distribution.—(See above) Roggeveld escarpment south of Calvinia, near Middelpos.

Flowering Time.—October–November.

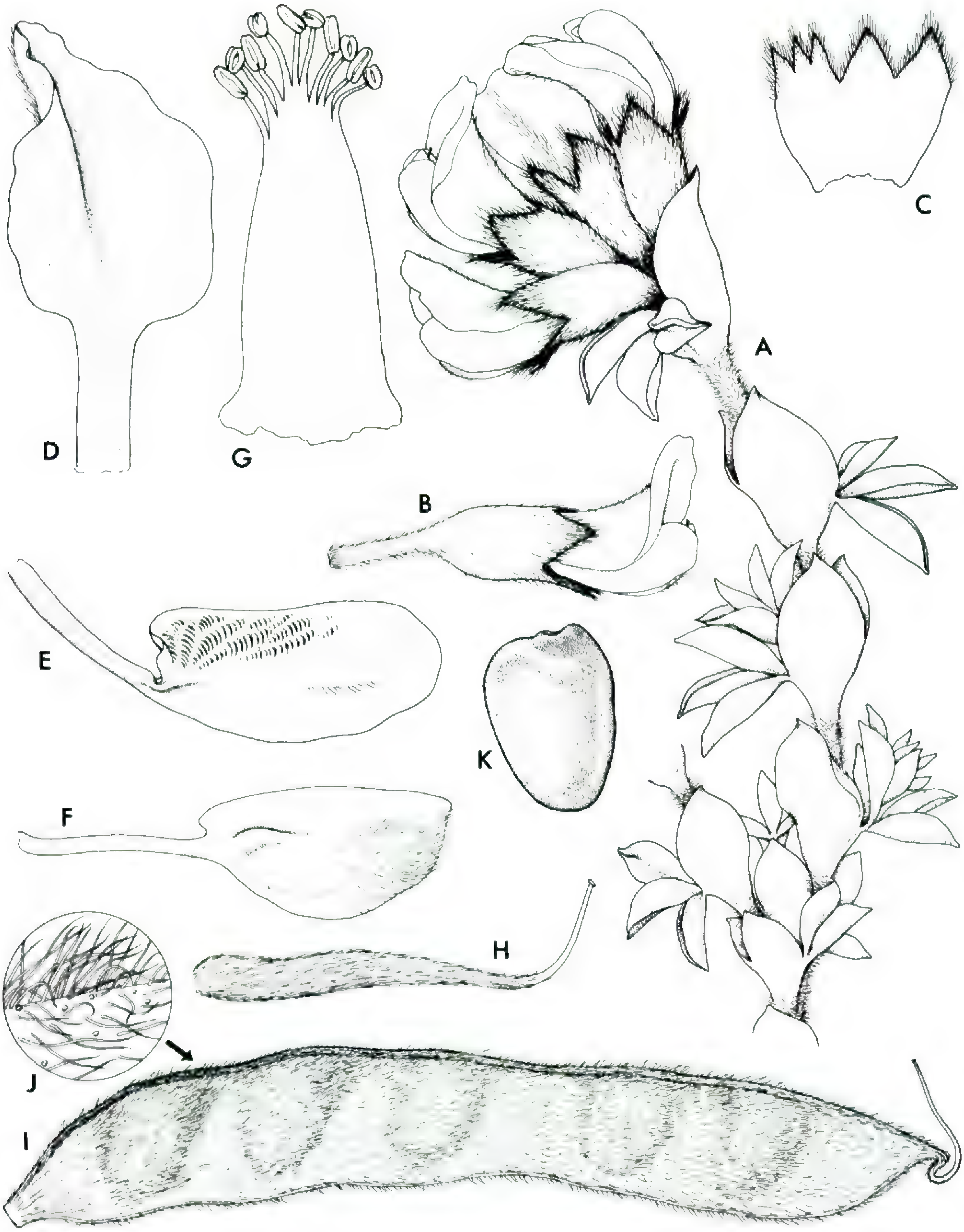

FIGURE 1. *Argyrolobium involucratum:* A. Inflorescence. B. Flower. C. Lower calyx lobes (A–C, ×2.5). D. Standard. E. Wing. F. Keel. G. Androecium. H. Gynoecium. I. Legume. (D–I, ×5). J. Detail of legume showing glandular hairs (×25). K. Seed (×10).

DISCUSSION

The type specimen of Thunberg's deviates from the richer material (*Goldblatt 4389, 4614*) in having a longer (up to 2.5 cm) internode below the uppermost leaf, and in the sheath-like stipular involucre enclosing the inflorescence. The pedicels also seem to be somewhat longer, but this may be due to difference in stage.

The morphology clearly indicates that this species—to whichever genus it belongs—is a typical member of the tribe Crotalarieae sensu Polhill (1976). Its foliage is mostly glabrous with the exception of the petioles, which are covered with villous hairs. It may be remarked that beneath the ordinary hairs on the petioles, as on the legume, there are short glandular hairs similar to those that occur in *Melolobium*.

The development of the stipules is exceptional: broad, ovate, fused to the basal part of the petiole, enclosing the stem, meeting on the leaf-opposed side and fused on this side for some millimeters at the base. This condition, somewhat reminiscent of that in the South American genus *Anarthrophyllum*, but no doubt developed independently of this, is also found in *Argyrolobium connatum*, a species with "silky-canescent" pubescence and paired flowers having "villous vexillum and carina."

The calyx is characteristic in having its three lower lobes fused into a "lip"-like structure, whereas the upper two are larger and separated from each other and from the lower "lip" by deeper incisions. This is a feature characteristic of *Melolobium* as well as *Argyrolobium* and is a common feature in the tribe Genisteae (sensu Polhill, 1976). The petals are typical of the tribe Crotalarieae, similar shapes being found in genera such as *Aspalathus* (Dahlgren, 1963), *Lotononis*, *Melolobium* and other genera. Also typical of the tribe Crotalarieae is the androecium, in which the filaments are fused to form a sheath with an adaxial slit, running to the very base of the filaments, on either side of the upper median stamen. This is wholly in agreement with genera such as *Aspalathus*, *Lebeckia*, *Wiborgia*, *Rafnia*, *Lotononis*, and *Melolobium*, while the Genisteae s. str. principally are characterized by a closed staminal tube. The anthers are alternately long-basifixed and short-dorsifixed, as is generally the case in the Crotalarieae.

The legume, finally, is linear and covered with short gland-hairs as well as ordinary hairs, as in *Melolobium*.

Thus, there seem to be some decidedly *Melolobium*-like features of the present species, and its position in *Argyrolobium* is challenged. It seems that *Argyrolobium* at least is a heterogenous genus as circumscribed by Harvey (1862) and also by Polhill (1976). This is even the more obvious, as the genus is included in the keys both of the tribe Crotalarieae and the tribe Genisteae in Polhill's treatise of the Genisteae s. lat.

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NOTES ON THE CYTOLOGY AND DISTRIBUTION OF *ANAPALINA, TRITONIOPSIS,* AND *SPARAXIS*, CAPE IRIDACEAE[1]

PETER GOLDBLATT[2]

Anapalina and *Tritoniopsis* are two closely related genera of Iridaceae subfamily Ixioideae, both restricted in distribution to the Cape Province of South Africa and both centered in the Cape Floristic Region. *Sparaxis,* also a member of subfamily Ixioideae is only distantly related to these two genera, and its range is restricted to the western Cape and adjacent karoo. Recent collecting expeditions to South Africa have enabled me to extend knowledge of the cytology and distribution of *Tritoniopsis* and of *Sparaxis,* and this new information is presented here.

Chromosome counts were made from root tip mitoses, squashes being prepared by the method outlined in other papers (Goldblatt, 1976; Goldblatt & Gentry, 1979).

TRITONIOPSIS AND *ANAPALINA*

CHROMOSOME CYTOLOGY

1. *Tritoniopsis.—Tritoniopsis parviflora* (Jacq.) Lewis $2n = 32$. S. Africa, Cape, near Baardscheerdersbos, Caledon distr., *Goldblatt 5385* (MO).

Tritoniopsis doddii (Lewis) Lewis $2n = 30$. S. Africa, Cape, Vogelgat, lower slopes near Hermanus, *Goldblatt 5387* (MO).

The only previous counts in *Tritoniopsis* are $2n = 32$ for four species, *T. leslei, T. lata, T. parviflora* and *T. unguicularis* (Goldblatt, 1971). The new count here for *T. parviflora* confirms the earlier report of $2n = 32$, but the count of $2n = 30$ in *T. doddii* is a new number for the genus. The somewhat specialized *T. doddii* may be an aneuploid species. Cytological preparations for this species, which has the small chromosomes characteristic of subfamily Ixioideae, are not perfectly clear, but a pair of large metacentrics are evident, and not seen in the karyotype of *T. parviflora*.

2. *Anapalina.—Anapalina caffra* (Ker ex Bak.) Lewis $2n = 32$, $32 + 1B$. S. Africa, Cape, southern Cape near Storms R. bridge, *Goldblatt 5214* (MO).

There are only two counts in the chromosome record for *Anapalina,* both $2n = 34$ (Goldblatt, 1971), for *A. nervosa* and *A. triticea.* The present count, $2n = 32$, for *A. caffra,* is thus the first report for the species and a new number for *Anapalina*. While this may represent aneuploidy in the genus, previous counts require confirmation. These were made using section techniques, which are known to yield preparations more difficult to analyze than squash methods employed here.

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RANGE EXTENSION FOR *TRITONIOPSIS FLEXUOSA* (L.F.) LEWIS

Tritoniopsis flexuosa is a rare, local endemic of the Caledon district, until now believed to be restricted in range to the lower slopes of Shaws Pass, south of Caledon (Lewis, 1952, 1959). It was first collected by Thunberg in 1774, who did not provide a locality for the species, and not again until 1937 when T. M. Salter collected leaves only, on Shaws Pass. G. J. Lewis collected flowering plants the following year, and was then able to relate Thunberg and Linnaeus fil's *Gladiolus flexuosus* to a known South African plant.

The species is very distinctive, both in leaf and flower and thus when I found a small population in leaf, with old, dry, inflorescences on the farm Mierkraal, ca. 12 km S of Bredasdrop, I knew at once that the species was indeed *Tritoniopsis flexuosa* even though the plants were some 60 km SE of the known range of the single population. The plants (*Goldblatt 5609* at MO) have the peculiar single basal leaf, produced before the flowers, with its remarkable filiform pseudopetiole ca. 4 cm long, and lanceolate-ovate lamina, cordate at base with two conspicuous nerves and undulate margins. Other features such as bract and fruit morphology also conform with Lewis' detailed descriptions (Lewis, 1952, 1959).

It seems likely that this rare summer flowering species may occur elsewhere between the two stations now known. Its late summer blooming period may be one reason why it is seldom recorded, for little collecting is normally done at this season, the driest and hottest time of the year in this region of mediterranean climate.

SPARAXIS

Sparaxis is a small genus of six species. It is fairly well known and was revised recently by myself (Goldblatt, 1969). A synopsis of the species and their geography was published in 1979 (Goldblatt, 1979) that essentially summarized the earlier paper.

At that time *Sparaxis pillansii* L. Bolus was believed to be a very narrow endemic of seasonally damp sites near the village of Nieuwoudtville at the northern edge of the Cape Floristic Region. A single record of the species from Driefontein, SW of Calvinia, some 35 mi to the east, *Marloth s.n.* was regarded as doubtful and requiring confirmation (Goldblatt, 1969). In 1980 I discovered a small population of *S. pillansii* in a damp gully on the lower slopes of the Hantamsberg, just north of Calvinia (*Goldblatt 5806*). The population is certainly native there, and the range of *S. pillansii* is thus extended from Nieuwoudtville eastwards some 40 mi. This record suggests that the Marloth gathering from Driefontein, not far distant, is in fact correct. *Sparaxis pillansii* thus appears to be a western karoo species rather than a marginal species of the Cape Floristic region. As far as is known, *S. pillansii* is still most common in the Nieuwoudtville area and although this is its present center today, it may well have evolved in the presently arid western karoo in the past when the climate there was more amenable.

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A REVISION OF *SYNGONIUM* (ARACEAE)

THOMAS B. CROAT[1,2]

ABSTRACT

Thirty-three species are recognized for *Syngonium* in this first published revision since that of Engler and Krause in 1920. *Syngonium* (now including *Porphyrospatha*) is the only member of the tribe Syngonieae (Araceae). The genus includes 4 newly described sections, sect. *Oblongatum* Croat, sect. *Cordatum* Croat, sect. *Pinnatilobum* Croat, and sect. *Syngonium* Croat, defined by leaf morphology, namely by blades basically oblong, cordate, pinnately lobed, and pedately lobed, respectively. Eleven new species are described: *S. chocoanum* (Colombia: Chocó), *S. dodsonianum* (Ecuador: Los Ríos), *S. foreroanum* (Colombia: Chocó), *S. gentryanum* (Peru: Huánuco), *S. glaucopetiolatum* (Costa Rica, Panama), *S. harlingianum* (Ecuador: Pastaza), *S. laterinervium* (SW Costa Rica, NW Panama), *S. llanoense* (Panama), *S. sparreorum* (Ecuador: Cotopaxi), *S. steyermarkii* (Guatemala and SE Mexico), *S. triphyllum* (Honduras to Panama).

The genus *Syngonium,* interpreted here to include the genus *Porphyrospatha,* is one of two genera of Araceae (the other being *Monstera*) with a center of diversity in Central America. The following revision of *Syngonium* includes 33 species of which 11 species are described as new to science. Three species are transferred to *Syngonium* from other genera, namely *Philodendron* (2 spp.) and *Porphyrospatha* (1 sp.).

Although the genus needs more field work, especially in South America, the present revision is the culmination of field work conducted in Central America and northern South America over the past decade.

HISTORY OF THE GENUS

The first species of *Syngonium* was described by Linnaeus as *Arum auritum* in his second edition of *Species Plantarum* in 1763. Other species of *Syngonium* were described by early botanical workers in the genera *Caladium* and *Xanthosoma.* The latter two genera, both neotropical in distribution, are members of the subfamily Colocasioideae but are now circumscribed as terrestrial, basically acaulescent genera with entire or pedatisect leaves. The genus *Arum,* in the subfamily Aroideae, as now circumscribed, is restricted to Europe and the Mediterranean region.

The name *Syngonium* was first used by Schott in 1829. By the time Schott published his *Synopsis Aroidearum* in 1856 there were 11 described species, the bulk of them having been described in that work. However, of those 11 species I recognize only 1 in this revision, namely, *S. auritum* (most of the species having been synonymized with the widespread *S. podophyllum*). Schott's (1860) *Prodromus Systematis Aroidearum* dealt with 20 taxa, of which only *S. schottianum, S. hoffmannii, S. wendlandii, S. salvadorense, S. podophyllum* var. *peliocladum, S. neglectum,* and *S. angustatum* are recognized by me. These new species were

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based on collections of H. Wendland, C. Hoffmann, F. M. Liebmann and A. S. Oersted in Mexico and Central America during the 1840s and 1850s.

The last revision of *Syngonium* was that by Engler & Krause (1920) published in *Das Pflanzenreich*. In that treatment two additional species were added (as now recognized) namely *S. hastifolium* and *S. macrophyllum*. The remainder of the species published on or before this revision by Engler have been either placed into synonymy or transferred to other genera.

The most important recent work with *Syngonium* was that by Birdsey (1955) who completed a detailed morphological review of the Central American and West Indian (in part) species for his doctoral thesis. Although this work was never published, the thorough anatomical studies remain an important contribution. In Birdsey's work a number of new species were described. Two of these species were subsequently described by Bunting (1966) and an additional one, *S. triphyllum*, is described in this paper. Bunting described a total of 6 recognized species during his work in Central America and in Venezuela. A single *Syngonium* described by E. Matuda is also recognized.

Most of the new species described in this work are relatively rare species collected in the past decade but a few rare species, such as *S. steyermarkii* and *S. laterinervium*, were collected as long as 30 years ago but not recognized.

Generic Relationships

Syngonium is typical of the subfamily Colocasioideae, whose members have in common articulated laticiferous tubes and leaves almost always having reticulated veins, with the secondary lateral veins joining into a collective vein between the primary lateral veins. In addition, all that have been studied in the field have milky sap.

Schott (1856) in *Synopsis Aroidearum* classified only the diclinous genera of Araceae. He separated these genera into Efilamentatae and Filamentatae, the latter containing only the genus *Stylochiton*. Efilamentatae was divided into two parts, Stenozeugmaticae and Pachyzeugmaticae, the latter divided into Gyminogoneae (pistillate flowers lacking staminodia) and Peristatogoneae (pistillate flowers with staminodia). Gyminogoneae was divided into 2 tribes, Caladiinae and Philodendrinae. Caladiinae contained 5 subtribes with genera as follows:

Subtribe Colocasiinae
- *Ariopsis*
- *Colocasia*
- *Remusatia*

Subtribe Alocasinae
- *Gonatanthus*
- *Alocasia*

Subtribe Peltandrinae
- *Peltandra*

Subtribe Syngonieae
- *Caladium*
- *Xanthosoma*
- *Acontias*
- *Syngonium*

Subtribe Problematicae
- *Anchomanes*
- *Zamioculcas*

The subtribes of Caladiinae were later reduced by Schott (1858) as follows:

Subtribe Colocasiinae
- *Ariopsis*
- *Remusatia*

Subtribe Syngonieae
- *Typhonodorum*
- *Hapaline*

Colocasia
Leucocasia
Gonotanthus
Alocasia
Peltandra
Subtribe Anubiadinae
Anubias
Caladium
Xanthosoma
Acontias
Synogonium
Subtribe Problematicae
Zamioculcas

Hutchinson (1932) arranged the family Araceae into 18 tribes and mistakenly over-emphasized the scandent habit of *Syngonium* in placing it with *Philodendron* in the subfamily Philodendroideae, which contains neither articulated laticiferous tubes nor milky sap and also lacks the reticulate-veined leaves of the subfamily Colocasioideae.

In the most recent complete revision of the subfamily Colocasioideae by Engler & Krause (1920) three tribes were included. The two smaller tribes were the Syngonieae with 2 neotropical genera, *Syngonium* and *Porphyrospatha* Engler and the Ariopsideae with the single Himalayan genus *Ariopsis* Nimmo. The third tribe Colocasieae with 5 subtribes contain 12 genera. The subtribe Steudnerinae with 12 species contains the genera *Steudnera* C. Koch, *Remusatia* Schott, and *Gonotanthus* Klotzsch. The subtribe Hapalininae contains only the genus *Hapaline* Schott with 5 species, and the subtribe Colocasinae contains only *Colocasia* Schott with 8 species. These first three subtribes are almost exclusively Asian in distribution. The subtribe Caladiinae with *Caladiopsis* Engler, *Caladium* Vent., *Aphyllarum* S. Moore, *Chlorospatha* Engler, and *Xanthosoma* Schott is exclusively neotropical and contains about 65 species. The subtribe Alocasiinae contains 2 genera, *Alocasia* Schott with 70 species in the Old World and *Schizocasia* Schott with 4 species in the Philippines, Indochina, and Australia.

The Ariopsideae is distinguished from the Colocasiinae and the Syngonieae by having the synandria of the staminate inflorescence united. The Colocasiinae is distinguished by unilocular ovaries with placentation basal, parietal or subcentral, whereas the Syngonieae has ovaries bilocular (or unilocular by abortion), the ovules being 1 or 2 per locule and anatropous. Syngonieae is also the only tribe in the subfamily with scandent plants.

Because of their neotropical distribution and similarly veined leaves, as well as the frequent presence of milky sap, certain members of the Caladiinae, namely *Caladium* and *Xanthosoma*, have been confused with *Syngonium*. Caladiinae is terrestrial, either acaulescent with subterranean stems or caulescent with short, usually erect stems, whereas *Syngonium* is always epiphytic, frequently with scandent stems.

The Genus *Porphyrospatha*

Engler (1879) distinguished *Porphyrospatha* from *Syngonium* because the fruits of *Porphyrospatha* supposedly were free from one another at maturity, whereas in *Syngonium* the fruits formed a syncarp. I now believe that this distinction was based on a misinterpretation of poorly preserved material. *Porphyrospatha* was based on *Syngonium schottianum* from Costa Rica, which has the typical syncarp of *Syngonium*. It is possible that Engler's interpretation of a genus with free fruits was based on an old fruiting inflorescence. These may

appear segmented, especially after drying, and it is doubtful that Engler ever saw fresh fruits of his proposed genus. Old syncarps have been observed which were partly eaten, perhaps pecked apart by birds, and such an inflorescence upon drying might well have the appearance of having distinct fruits. [See for example *Croat 25542* (MO).] Unfortunately, it is not possible to restudy the material seen by Engler, since the only material apparently seen by him was a collection of Wendland from Costa Rica, which is no longer extant. The illustration of this species in Berlin shows an inflorescence in an intermediate stage of development and certainly not in mature fruiting stage.

Morphology

Stem

Syngonium is characterized by polyphyllous sympodial growth with an elongate shoot and no branches. After the shoot terminates in an inflorescence or a series of inflorescences, a single branch arises from the lateral bud, two nodes back from the apex (Madison, 1978). The stem branching pattern as reported by Engler (1877) is as follows:

```
etc. (up to 7 inflorescences depending on the species)
  ↑
Prophyll
  ↑
Inflorescence
  ↑
Prophyll                                      Penultimate Leaf (etc.)
  ↑                                                  ↑
Inflorescence                                       Leaf
  ↑                                                  ↑
Prophyll ←———    Inflorescence                      Leaf
                      ↑                              ↑
                 Ultimate leaf                      Leaf
                      ↑                              ↑
               Penultimate leaf ———→             Prophyll
                      ↑
                    Leaf
                      ↑
                    Leaf
                      ↑
                    Leaf
                      ↑
                  Cotyledon
```

The pattern depicted here is indefinitely repeatable, limited only by change in the ecological conditions that allow flowering. (See also section on Growth Habits.)

Stems may initially be only a few mm diameter in juvenile plants but up to 6 cm diameter in adult plants. *Syngonium* stems probably average 1 to 2 cm diameter. Stems are invariably green and presumably photosynthetic in juvenile plants, but the epidermis soon loses its color on adult plants (usually within 1 node below the inflorescence). The possibility of having photosynthetic tissue in the creeping phase of growth where internodes are elongate and leaves are small (see section on GROWTH HABITS) would be important ecologically.

In general the stems of *Syngonium* are unbranched though branching sometimes occurs, especially if the stem has been injured. Generally, climbing stems have elongated internodes. The internodes are often appreciably shorter on flowering portions than elsewhere. Some species, especially those species with thicker stems, such as *S. macrophyllum, S. crassifolium, S. schottianum* and *S. sagittatum,* may have the internodes quite short on flowering segments.

Stem segments are terete or more commonly oval in cross-section and have a shallow groove on one side above the axillary bud. This generally is diminished or absent distally. Birdsey (1955) reports a multiseriate epidermis in *Syngonium* with the developing stem near the apical meristem having only a single layer of cells and sections distal to the apical meristem having 3 or more layers of epidermal cells. Part of these layers may be suberized but at least the innermost is not suberized. Birdsey (1955) reports that it is not yet known whether this multilayered tissue arises from the epidermis or underlying collenchyma cells.

Stems are to some extent flexible but, if bent, the outer epidermis often cracks free. Even in undisturbed plants, the outer epidermis often becomes cracked and peels. In such cases the outer epidermis is generally brown or yellowish with the underlying epidermal cells green or olive green. The color of the epidermis is sufficiently variable to provide useful specific characteristics. For example, the outer epidermis of *S. erythrophyllum* always dries a characteristic brown only a short distance from the stem apex. Drying plant collections invariably causes shrinkage of the stem with the result that herbarium specimens have the outer epidermis cracked or fissured and often peeled free from the stem.

In the case of *S. angustatum* the epidermal cells are pushed out by underlying cells to provide rough spots visible to the naked eye (Birdsey, 1955), while the excrescences of *S. podophyllum* var. *peliocladum* are very large, providing the chief taxonomic characters for its separation from *S. podophyllum* var. *podophyllum*.

Another useful taxonomic character involving the stem is the presence or absence of a waxy layer, although the character does not necessarily maintain itself throughout the range of a species. For example, the stems of *S. podophyllum* in Mexico are glaucous and are useful there in separating it from *S. angustatum,* but in Panama and in South America the stems are never reported to be glaucous.

The glaucous condition is also present on other parts, especially the peduncle and the fruits, e.g., in *S. chiapense* and *S. macrophyllum*. The glaucous peduncles of *S. angustatum* are useful in separating it from *S. podophyllum*.

Stem anatomy was dealt with briefly by Van Tieghem (1867) and will be dealt with more completely in work underway by R. Keating of Southern Illinois University, Edwardsville. Birdsey (1955) also presents a thorough survey of stem anatomy.

Stem cross-sections of *Syngonium* show a well-defined layer of collenchyma (cortex) beneath the epidermal layers with a poorly defined boundary lacking between the cortex and the central vasculated region of the axis (Birdsey, 1955). Starch grains are randomly distributed throughout the parenchyma of both the central cylinder and the cortex, and idioblasts containing raphides as well as cells containing druses are present, though in lower frequency than in the petioles (Birdsey, 1955). The stem of *Syngonium* lacks a well-defined pith and has the scattered vascular bundles characteristic of monocots. Always present in the stems of *Syngonium* are articulated laticiferous cells, i.e., secretory cells, which are placed end-to-end, forming a continuous tube with numerous branches and anastomoses (Birdsey, 1955). The contents of the cells are rich in tannins as well as latex (Solereder & Meyer, 1928).

ROOTS

Adventitious roots of two types emerge just below each node of the stem. In addition to a number of skototropic clasping roots, whose main function is that of holding the plant to its support, there is a single feeding root that is positively geotropic and diverges from the stem at an angle that puts it into a position to absorb nutrients some distance from the plant (Birdsey, 1955). The anatomy of these roots differ at least quantitatively (Birdsey, 1955), with the feeding root having greater overall diameter, a proportionally larger central cylinder, and proportionally larger vessels.

LEAVES

Syngonium phyllotaxy is reported as $^2/_5$ divergence (Engler, 1877), though the arrangement may be obscured by the slight twisting of the petioles (Birdsey, 1955).

The petiole of *Syngonium* is always conspicuously sheathed from about the middle to near the apex, generally between the middle and the upper $^4/_5$ of the petiole. The sheath functions in protecting the newly emergent leaves and the inflorescences. The sheath is generally very broad, especially at the base, and the two sides are generally quite unequal in height. The apical portion of the sheath is often free-ending, and the free part varies from acute to rounded or emarginate at the apex. The petiole of section *Oblongatum* differs in being proportionately broader and extends often beyond the base of the blade.

The petioles have a uniseriate epidermis, with numerous intercellular spaces (Birdsey, 1955). The vascular bundles are irregularly scattered throughout the fundamental tissues. Perhaps owing to the numerous intercellular lacunae, the petioles of *Syngonium* are soft and can be easily crushed in comparison to other aroid genera such as *Anthurium*. The cross-sectional shape of the free portion of the petiole beneath the blade often has taxonomic significance. Although all are characterized by being rounded on the abaxial side and most have a single more or less conspicuous adaxial rib, the rib varies from being almost absent in the case of *S. chiapense*, *S. neglectum*, and *S. auritum* to quite noticeable in *S. podophyllum* var. *peliocladum*, *S. macrophyllum*, and *S. salvadorense*, to noticeably acute in *S. angustatum*, *S. triphyllum*, *S. wendlandii*, and *S. hoffmannii*.

In some species the lateral adaxial margin of the petiole is also ribbed. This is apparent in *S. hoffmannii* and *S. wendlandii* but especially in *S. triphyllum*.

The petioles of juvenile leaves often differ remarkably from that of the adult and have a greater tendency to be canaliculate rather than 1-ribbed as in the adult leaves.

The leaf blade morphology of *Syngonium*, as in many other genera of Araceae, is quite variable. Species often begin flowering before the full course of maturation takes place in leaf development. For example, young adult plants may have fewer leaflets per leaf than older plants. This has created a situation where species have been described as new because the adult leaves were unlike plants which had previously been described.

The leaves easily fall into four basic types, and it is along these lines that the sectional classification of the genus is arranged.

Section Syngonium.—By far the most common leaf type in the genus is that of section *Syngonium* with trisect or pedatisect adult leaf blades. Leaf blades range from the strictly trisect blades of *S. gentryanum* to the more highly divided blades of *S. podophyllum*, which vary from trisect to 11-pedatisect. Though the condition is not necessarily a strict matter of maturity, older, more mature plants in any population tend to be more highly divided. Any individual may have considerable variation in the degree of lobing of the leaf depending on where the leaf occurs on the stem. The higher up the stem, generally, the more highly lobed or segmented the leaf becomes. As mentioned in the section on STEMS, the seedling leaves of all species are entire. Generally the seedling leaves are ovate or elliptic, and frequently they are also weakly lobed at the base. The intermediate climbing leaves are always more conspicuously lobed at the base. The leaves of such intermediate, pre-adult climbing forms are generally conspicuously hastate or sagittate. It is during this pre-adult climbing stage that species are most difficult to distinguish from one another, since nearly all the species in section *Syngonium* have leaves that are remarkably similar. However, even at this stage, differences between species begin to emerge. Some species, such as *S. triphyllum*, have posterior lobes that are narrow and are directed almost perpendicular to the median lobe. The abruptness of change between an entire leaf with prominent basal lobes and a 3-lobed leaf varies considerably from species to species. In some species all intermediate stages are easily found, whereas in other species the plant seems to switch from an entire pre-adult leaf to a 3-lobed or 3-parted pre-adult leaf very quickly with no evidence of intermediate leaf forms. The general pattern of change extend from a more or less sagittate blade, to a hastate blade, to a 3-lobed blade with the posterior lobes very constricted near the base. The development proceeds to where the posterior lobes become lateral leaflets, i.e., they become completely free of the median lobe.

The lateral segments or leaflets are invariably inequilateral and in most cases the outer half of the segment or lobe is much wider and conspicuously auriculate at the base. The degree to which the auricle develops is very variable from plant to plant, even in the same species (particularly true of species like *S. podophyllum*), but it is often sufficiently consistent in a species to be of taxonomic value.

Leaf development of five or more pedatisect leaves invariably proceeds with the pinching off of an auricle to produce another segment or leaflet which in turn

goes through the same process to produce still another pair of segments or leaflets.

The degree of separation of the segments or leaflets is an additional taxonomic character in some species (and not in others). Some species consistently have leaflets free from one another with exposed sections of the rachis dividing the leaflets. In morphologically variable species, such as *S. podophyllum*, the degree of separation of the leaflets is highly variable, even at the populational level with leaves varying from those with united segments to those with distinct leaflets.

Section Cordatum.—In this section the leaves are entire with generally conspicuously developed posterior lobes. The overall leaf shape may be ovate or oblong-ovate or rarely hastate, and the anterior lobe is sometimes weakly constricted near its base. The section is the second most common and includes those species (among others) that Engler placed in his genus *Porphyrospatha*. Seedling leaves are similar to those of section *Syngonium* and soon become ovate-elliptic with small posterior lobes, but instead of becoming more 3-lobed, they begin to assume the shape of the adult blade and merely get larger. In section *Cordatum* there are no leaves with distinctly intermediate phases, which are so variable and interesting in section *Syngonium*.

Section Oblongatum.—The species in section *Oblongatum* differ markedly from all others in the genus because of the oblong to oblong-elliptic to ovate-elliptic leaf blades and petioles, which are broadly sheathed to the apex with the emarginate free portion of the sheath often extending beyond the base of the blade. In this section the juvenile leaves are almost identical to the adult leaves, differing only in being much smaller. Intermediate stages are much like the adult blade.

Section Pinnatilobum.—This section is represented by *S. steyermarkii*, the only incised-lobate species in the genus. Juvenile leaves are ovate, soon becoming subcordate at the base and developing sinuate margins laterally. As the blade matures, it becomes increasingly more deeply lobed and more conspicuously lobed at the base until it assumes its adult form, which looks vaguely like the common *Philodendron radiatum* Schott with incised-lobate leaves.

Leaf blade venation of *Syngonium* easily characterizes it as a member of the Colocasioideae. The venation type is the brochidodromous type (Dilcher, 1974), and the primary lateral veins (i.e., secondary, see Croat & Bunting, 1979), after extending laterally from the midrib toward the margin, join into a collective vein which extends to the apex roughly parallel to the margin. In *Syngonium* there are always 3–5 separate collective veins. The primary (inner) one, being the largest, is initiated by one of the lowermost primary lateral veins. Successively smaller collective veins, located at smaller distances from the blade margin, arise from progressively lower primary lateral veins or even weak secondary veins branching off the midrib. Frequently the 4th and especially the 5th collective vein are so near the margin that they cannot be seen with the naked eye.

The origin of the primary lateral veins is usually acute near the base, often becoming more obtuse toward the apex and rarely arising at nearly right angles to the midrib.

One of the characteristics of *Syngonium* and other members of the Coloca-

sioideae is the presence of conspicuous reticulate venation. Tertiary veins can arise from the primary lateral veins (i.e., secondaries) in which case they orient toward the margin and become parallel to the primary lateral veins, or they can arise directly from the midrib. The tertiary veins merge distally and give rise to quaternary veins. The quaternary veins are found irregularly between the tertiary veins and at oblique angles, randomly oriented. The quaternaries in turn give rise to the lowest order of veins, namely the quinary veins which form the areoles. The areoles are 3-, 4- or 5-sided and lack a free-ending veinlet. Both the 4th and 5th order veins are restricted to the adaxial plane of the blade (Birdsey, 1955). An unusual feature of the quaternary veins of *Syngonium* and other Araceae such as *Xanthosoma* is that they may cross over a series of tertiary veins before joining with another vein (Birdsey, 1955).

Laticiferous cells are often very prominent in the leaf tissue, with two series of laticiferous cells paralleling each vein, sometimes even up to the 5th order of veins (Birdsey, 1955).

REPRODUCTIVE STRUCTURES

The inflorescences of *Syngonium,* though always terminal, appear to be axillary because after the inflorescences are produced, the continuation shoot, which arises from the penultimate leaf, displaces the inflorescence to the side and overtops the inflorescences. Inflorescences may be solitary or several but are interspersed with bicarinate bracts called prophylls. A number of species, such as *S. angustatum, S. podophyllum,* and *S. macrophyllum,* produce between 6 and 11 inflorescences, whereas many species produce only 2 inflorescences, and some may produce a solitary inflorescence. The number of inflorescences that persist and produce mature fruits is frequently fewer than those that reach anthesis. Some are perhaps not pollinated or are removed before maturity for some reason.

Inflorescences are nearly always erect and the peduncles are generally obtusely 3-sided or subterete with an obtuse rib on one side. The peduncle, often relatively short at anthesis, generally elongates substantially in fruit and becomes recurved, no doubt due to the heavy weight of the fruits.

The unopened spathe is convolute and very tightly closed over the spadix, generally exceeding the spadix by $^1/_6$–$^1/_3$ its length. The spathe is often conspicuously constricted about midway, separating the spathe tube from the spathe blade. At flowering time the spathe unfurls and generally forms a more or less hemispherical cup behind the spadix. By the time the spathe is fully open, it is generally white or creamy white, at least on the inner surface of the spathe blade, though the blade and more frequently the inner surface of the spathe tube may be colored or at least tinged with red or violet. In some cases, such as *S. neglectum,* the spathe may be reflexed backward, which more fully exposes the spadix. Though the lower convolute part of the spathe (the tube) is rarely fully opened, it opens far enough to give easy access to the pistillate flowers for pollinators. The spathe remains open for 2–3 days and then recloses over the spadix. The blade portion of the spathe then soon withers and often promptly falls free. In other cases the old dried spathe blade persists until later stages of fruit de-

velopment. The spadix is divided into three sections. Staminate flowers occupy most of the apical $^4/_5$ or more of the spadix. The lowermost section is occupied by the pistillate flowers. The basal part of the staminate spadix is made up of sterile staminate flowers, and these may form a distinct segment, or it merges imperceptibly with the staminate flowers. Flowers are arranged in a series of close spirals.

The pistillate part of the spadix is generally much narrower than the staminate part and is generally greenish, though sometimes pale orange. Length varies from 7–48 mm.

Each pistillate flower consists of two fused carpels (rarely three). The flowers are in turn fused into a single unit that later matures into a syncarp. Each locule usually has one ovule but may rarely have two (Birdsey, 1955). Ovules are anatropous and placentation is basal.

Birdsey (1955) describes four stigma types: (1) discoid, characteristic of *S. angustatum, S. auritum, S. chiapense, S. macrophyllum,* and *S. podophyllum*; (2) bilabiate (2-lobed or fused together in a ring), characteristic of *S. hoffmannii* and *S. salvadorense*; (3) orbicular, restricted to *S. wendlandii*; and (4) cupulate, restricted to *S. triphyllum.*

Sterile staminate flowers are usually roughly the same size as the fertile staminate flowers but more irregular in shape and generally more widely spaced. Sometimes the irregularity in shape results from a fusion of two flowers.

Fertile staminate flowers of *Syngonium* are made up of usually 4 (rarely 2, 3 or 5), nearly sessile anthers. The anthers are fused to varying degrees into a synandrium. The latter is truncate at the apex and sometimes depressed medially. The margins of the synandrium are rhombic, pentagonal, hexagonal, or irregular in outline. Sometimes the margin is also crenulate. Birdsey (1955) divided pollen grains into three distinct types: (1) spiny, characteristic of *S. angustatum, S. auritum, S. chiapense, S. macrophyllum,* and *S. podophyllum*; (2) smooth, characteristic of *S. hoffmannii, S. neglectum, S. salvadorense,* and *S. wendlandii*; and (3) knobby, characteristic of only *S. triphyllum.*

Cytology

Chromosomal studies with the Araceae have been fairly extensive for a tropical family, perhaps owing to the fact that the family is so widely cultivated. The most extensive reviews of chromosomal variation in the family are those by Marchant (1970, 1971a, 1971b, 1972). Somatic chromosome counts range from $2n = 22$ to $2n = 140$ for the family, and there is considerable diversity in the size of chromosomes. Jones (1957) indicates that $x = 6$ and 7 are the basic numbers for the family and that others have been derived. Larsen (1969) and Hotta (1971) believe that the most common base number is $x = 7$, followed by $x = 13$. Jones (1957) suggests that $2n = 26$, 30, and 34 are amphidiploid numbers that arose from hybridization and doubling of diploid species. Polyploidy appears to have played an important role in the evolution and speciation of the family.

Marchant (1970) reported base numbers of $n = 7$ for those members of the Colocasioideae which he investigated, namely *Remusatia, Alocasia, Colocasia, Xanthosoma, Caladium,* and *Ariopsis. Syngonium* has had counts of $2n = 24$ (Pfitzer, 1957; Marchant, 1970), $2n = 26$ (Marchant, 1970), $2n = 28$ (Sharma, 1970), and $2n = 30$ (Marchant, 1970).

Phenology

Phenological behavior of flowering and fruiting in *Syngonium* is poorly understood because no long-term observations have been made. From an analysis of herbarium material (now very abundant for some species) it can be stated that some species (perhaps most) flower over a relatively long period of time each year. Notwithstanding the fact that irregular collecting patterns could contribute to the results, it appears that some species are to some extent seasonal in their flowering behavior. For example, *S. angustatum* and *S. macrophyllum* show greatest flowering in the first part of the rainy season (beginning about May) in Central America, with some flowering during the dry season, but no flowering in the latter part of the rainy season.

Some species appear to be bimodal in their flowering behavior with tendencies to flower in the beginning of the dry season and the rainy season.

Pollination

Though no pollinators have been reported in the literature for *Syngonium* species, there seems to be little doubt that the genus has the same type of pollination syndrome already known for *Philodendron, Dieffenbachia* (Croat, 1978), and *Xanthosoma,* which are known to be pollinated by large awkward scarab beetles of the subfamilies Rutelinae and Dynastiniae. T. Ray (pers. comm.) reports that *S. triphyllum* is pollinated by the genus *Cyclocephala* (Dynastiniae) in Costa Rica. In such cases the behavior of the spathe and spadix are important and in all probability *Syngonium* is thermogenetic in the same way as *Philodendron* (Sheridan, 1960), *Monstera* (Sheridan, 1960; Madison, 1977), *Symplocarpus, Arum, Arisaemum, Amorphophallus, Biarum* and *Sauromatum* (James & Beevers, 1950; Smith & Meeuse, 1966; Knutson, 1972). In these cases it has been shown that temperature increase in the spadix is due to rapid oxidation of starch (James & Beevers, 1950; Beevers, 1950; Hatch & Millard, 1957; Hess & Meeuse, 1968a, 1968b; Knutson, 1974; Nagy et al., 1972).

Flowers of *Syngonium* are markedly protogynous, becoming receptive 1–2 days before the staminate flowers shed pollen. They are already receptive by the time the spathe opens. At this stage the spathe is broadly opened and access to the pistillate flowers is easy. Presumably pollinators enter the spathe at this time and visit the pistillate flowers while the staminate flowers are not yet open. Usually, by the beginning of the second day the pollen has begun to emerge in stringy masses from between the synandria, and the pistillate flowers are no longer receptive. By this time the spathe tube is much contracted and nearly closed, perhaps forcing an entrapped beetle to crawl over the pollen-covered spadix, as in the case of *Dieffenbachia* (Croat, 1978).

Infructescence

After pollination, the spathe tube becomes tightly reclosed and rots off, taking with it the remaining staminate flowers. Generally the dehiscence of the spathe tube follows a smooth line of thickened, often raised tissue, which is not readily apparent when the spathe first opens but which may become conspicuous by the time the spathe is closing. Part of the staminate spadix, generally including all of the sterile staminate flowers, is closed into the spathe tube. This material even-

tually rots but remains within the spathe tube. As in the case of *Alocasia pubera* (van der Pijl, 1933), the staminate flowers of *Syngonium* may be good places for insects to oviposit since part of the staminate spadix remains enclosed in the spathe tube and would provide an ideal hatching ground for larvae.

At maturity of the syncarpous fruit, the spathe tube is usually colored on the exterior, even though it is usually green at the time of flowering. The spathe tube usually also opens to expose the syncarp. The syncarp is generally pale, with brown flecks representing the original epidermal tissue. Sometimes the spathe tube breaks up and turns inside out, with its bright, colorful interior exposed against the white syncarp, e.g., *S. triphyllum*. Birdsey (1955) reported that only two species, namely *S. wendlandii* and *S. mauroanum*, had syncarps that matured white, but I found this to be true also for *S. triphyllum*. In such cases the fruits might be adapted for bird dispersal, since they would be highly visible and could be pecked open by birds. In most cases, however, the fruits seem better suited for mammal dispersal (presumably monkeys) because they are not very colorful, yet they are fragrant.

Each fruit of *Syngonium* contains 50–100 or more seeds. These are generally somewhat ovoid or cylindroid, usually 5–10 mm long and 3–6 mm in diameter, with both ends rounded. The pericarp is usually brown or black with the whole interior white and moderately soft. Germination of the fruits is prompt and viability of the seed is lost promptly if they are allowed to dry out.

GROWTH HABITS

A detailed study of growth behavior has been carried out on several species in Costa Rica by T. Ray (Harvard University). Only the general aspects of growth behavior will be reported here. Juvenile plants of a species of *Syngonium* are often extremely abundant, but there seems to be no correlation between the abundance of seedlings and the abundance of adults. In some cases adults are frequent and in other cases they are rare.

After germination of the seed, which is always in the soil, the plant remains in a rosette stage for a considerable time, the stem being slender with very short internodes. Leaves, at first ovate, are soon at least weakly lobed at the base. (A discussion of leaf development has already been made under the section on leaves.) Later (at least in some species), the stem elongates rapidly and growth is skototropic (Strong & Ray, 1975), i.e., the stem grows toward the darkest area available. Stem diameter may initially be only a few millimeters in this creeping phase, but internodes are elongate and leaves are much reduced. After the stem reaches a tree, it switches its physiology dramatically and begins to grow up the trunk toward the light. The stem continues up the trunk with relatively elongate internodes but also grows in girth and produces larger leaves. At this stage, the leaves (depending on the section) take on a different form. For example, climbing leaves of section *Syngonium* become sagittate or hastate. As the stem climbs, it becomes larger in girth and produces larger leaves and often stems with shorter internodes. Ultimately the plant produces adult foliage, which, depending on the species, can continue to be modified as the plant gets older or bigger. For example, pedatisect species tend to add more leaflets as they get larger.

All species of *Syngonium* are climbers and generally hemiepiphytic, though

plants may survive with all apparent connections to the ground severed. Older plants particularly have good development of an adventitious root system, which can trap both water and nutrients.

Though it has fewer growth forms than *Monstera,* described by Madison (1977), the genus *Syngonium* has a wide range of variation in growth form. In general, the larger the stem of the adult plant, the shorter will be its internodes at time of flowering. The stem diameter of all species ranges from 1.7 cm at the smallest extreme to 2.3 cm at the largest extreme. Species with very slender stems tend to occupy disturbed habitats such as fence rows, and they tend to flower readily and frequently but generally produce fewer than 3 inflorescences. For example, species with stem diameters averaging about 1.5 cm in diameter produce an average of 3 inflorescences per axil, whereas species with stem diameters averaging 3.8 cm have an average of 4.8 inflorescences per axil. There are notable exceptions, such as *S. angustatum* with stem diameters of up to only 1.5 cm but with usually up to 7 inflorescences per axil. At the other extreme are such species as *S. occidentale* with stem diameters to 3 cm but only a solitary inflorescence per axil, and *S. sagittatum* with stem diameters to 4 cm and up to 3 inflorescences.

Internode length at flowering time is often very great, sometimes exceeding 12 cm. Some species such as *S. laterinervium* tend to branch readily and festoon the plant upon which they are growing. Species with stout stems, such as *S. schottianum* and *S. macrophyllum,* are frequent only in large trees and tend to flower less frequently but generally produce more inflorescences. Adults of such species are generally rarer, perhaps being capable of maturing only in trees of certain height. Certainly, such species are never capable of reaching maturity on or near the ground.

Most species of *Syngonium* have medium-sized stems and though their internodes are somewhat shortened at flowering time, they continue to elongate rapidly so that a considerable distance exists between a mature infructescence and a new inflorescence.

The genus *Syngonium* goes through modifications in its growth much like those in *Monstera* (Madison, 1977). Most species rarely branch except when a plant is damaged or when it outgrows its support and begins to fall. When the stem of an adult plant begins to droop from its support, it changes its growth habits to produce narrower, longer internodes and smaller leaves. This, of course, allows the plant to put more of its growth into elongation in order to more quickly reach a new source of support. Once the new support has been found by creeping across the forest floor, the stem begins to climb once more and again modifies its growth to produce a succession of intermediate pre-adult leaves and adult leaves. The pattern can be repeated endlessly.

Geography

The center of diversity for *Syngonium* is in Costa Rica and Panama, which together have a total of 16 species. Costa Rica has 13 species while Panama has 11 species. Mexico is a secondary center of diversity with 8 species. Middle America (Guatemala to Costa Rica) has 8 species and the West Indies proper have but a single species (with another in Trinidad).

The most common and widespread species is *S. podophyllum* which ranges from Mexico to Brazil. Except for *S. macrophyllum*, most of the remainder are much less wide ranging and many, such as *S. glaucopetiolatum*, *S. gentryanum*, *S. hastifolium*, *S. laterinervium*, *S. llanoense*, *S. occidentale*, *S. podophyllum* var. *peliocladum*, *S. sagittatum*, *S. sparreorum*, and *S. steyermarkii*, are believed to be geographically isolated. Some, such as *S. mauroanum*, occupy special, restricted life zones while others such as *S. podophyllum* and *S. hoffmannii* occupy a wide variety of ecological habitats.

There are relatively few species of *Syngonium* in South America, though admittedly South America has been less well explored. In addition to the widespread *S. podophyllum*, which occurs in all parts of tropical South America, there is only one other species, *S. macrophyllum*, which ranges into South America from Central America. There are 11 species that are endemic to South America.

It is possible that *Syngonium* was a component of the remnant Paleogene tropical North American flora, as was suggested by Madison (1977) for the genus *Monstera*. Representatives of all sections of *Syngonium* are present in Central America, whereas only the two more common sections *Syngonium* and *Cordatum* are represented in South America. In addition, both of these sections are much better represented in Central America.

The distribution of *Syngonium* species does not show any of the disjunct distributional patterns for Central America that are exhibited by *Monstera* (Madison, 1977). Except for the three species of *Syngonium* already mentioned, which range from Mexico to Costa Rica or beyond (i.e., *S. angustatum*, *S. macrophyllum* and *S. podophyllum*), all other species in Central America are restricted either to Mexico or to Costa Rica and Panama.

Indicating that the paucity of *Syngonium* species in parts of Central America may be due to undercollecting is the fact that W. D. Stevens, now working on the *Flora of Nicaragua*, has already added *S. schottianum* to the flora of Nicaragua. It was previously thought to be restricted to Costa Rica and Panama.

The suggestion that Mexican species have long been isolated from those of Costa Rica and Panama is supported by the fact that only 3 Mexican species reach Panama, these being *S. angustatum* and the two widespread species *S. podophyllum* and *S. macrophyllum*, which range to South America.

Evidence that there may have been a long separation of populations of Mexican and Costa Rican or Panamanian species can be seen in the morphological variation among Mexican and Costa Rican populations of the two most widespread species in Central America. Both *S. podophyllum* and *S. macrophyllum* populations in Costa Rica and Panama differ in many ways from those in Mexico. These differences are discussed in the commentary following each species.

Infrageneric Classification

No previous worker has presented a sectional classification for *Syngonium*. This may be because until recently, two of the four sections I am proposing had not yet been discovered. *Syngonium crassifolium* and *S. schottianum* have both juvenile and adult leaves distinctly different from any species Engler & Krause (1920) included in their revision of *Syngonium*, but these two species were placed in a distinct genus (albeit presumably based on other characters, see section

discussing the genus *Porphyrospatha*). Nevertheless, Engler and Krause did include in their revision two species with adult leaves that were not the typical trisect or pedatisect leaves of section *Syngonium*. These were *S. hastifolium*, which in every other respect is like a juvenile plant of *S. podophyllum*, and *S. reticulatum*, now known to be a species of *Xanthosoma*.

Apparently the juvenile phases, which help to understand sectional differences, were not available to Engler. Nevertheless, the sectional classification I am creating is most readily recognized in the adult foliage, although there are corollary differences in the juvenile and pre-adult phases of growth.

I divide *Syngonium* into four sections based on the shape of the adult lamina.

Section Syngonium: Leaves trisect or 5–11-pedatisect. This section is by far the largest and most variable. It is also the only section with any truly widespread species. The species exhibit marked heteroblastic development, with changes in leaf development in the juvenile, creeping, climbing, and adult phases. These are described in detail under the heading LEAVES.

Section Cordatum: Leaves entire and with conspicuous posterior lobes. This section is the second largest section in the genus. Some of its species are relatively widespread. All (except perhaps *S. hastifolium*) are thick-stemmed, slow-growing hemiepiphytes that have juvenile leaves similar to the adult forms, only smaller.

The section is represented by five species, three of which are restricted to Central America. Juvenile leaf phases are ovate-cordate and intermediate stages begin to approach the adult shape with no major modifications. One species in section *Cordatum*, *S. chiapense*, occasionally has broad, rounded lobes separated somewhat from the posterior lobes. This tendency to produce auricles at the outer edge of the posterior lobes is characteristic of section *Syngonium* and reflects the relationships of these two sections. Nevertheless, *S. chiapense* has the entire, ovate-cordate leaf blades characteristic of section *Cordatum*.

Section Oblongatum: Leaves entire, elongate, the petiole broadly winged to the apex. This section differs not only in the shape of its leaves but in having a petiole that is broadly sheathed its full length with a free-ending ligule extending generally beyond the base of the blade. Juvenile leaves differ little from the adult except in size. The section is represented by two species, *S. llanoense* from the Isthmian region of Panama and *S. armigerum* from Costa Rica.

Section Pinnatilobum: Leaves deeply incised-lobate; petiole sheathed to about the middle; juvenile leaf blades entire, more or less ovate, cordate at the base; intermediate leaves increasingly incised. The section is represented by a single species, *S. steyermarkii*, from Mexico and Guatemala.

TAXONOMIC TREATMENT

Syngonium Schott, Wiener Z. Kunst 3:780. 1829. TYPE: *Arum auritum* L. = *Syngonium auritum* (L.) Schott.

Porphyrospatha Engler in A. DC., Monogr. Phan. 2:289. 1879. TYPE: *Syngonium schottianum* Wendl.

Epiphytes or hemiepiphytes; sap of most parts milky; stems scandent or short-creeping, usually unbranched, the internodes long or short, the nodes usually rooting heavily; juvenile plants usually terrestrial, the first blades ovate to elliptic, simple, with succeeding stages usually sagittate and climbing; adult leaves simple

or variously divided, trisect to pedatisect with 5–11 leaflets, rarely incised-lobate; petioles sheathed in part, rarely throughout their length, the upper part subterete, usually with an obtuse medial rib; simple blades usually ovate, sometimes oblong-elliptic, frequently ± sagittate; blades usually moderately thin, the median segments usually more or less equilateral, the lateral segments of trisect or pedatisect blades often conspicuously inequilateral and auriculate; primary lateral veins spreading, forming up to 3 or more collective veins.

Inflorescences 1 or more per axil; peduncles erect in flower, pendent in fruit, commonly rounded on one side, obtusely angular on the other side; spathe tube ovoid to ellipsoid, green at anthesis, frequently tinged with purple, often red, orange or yellow in fruit, usually reopening to expose the syncarp, sometimes brightly colored within at maturity; spathe blade white to greenish white and opening broadly at anthesis, usually ovate-elliptic, often acuminate at the apex, normally much constricted at the base, always drying soon after anthesis, usually deciduous; spadix much shorter than the spathe, the basal pistillate part cylindrical to truncate-conical, green to orange, the apical staminate part longer than the pistillate part, clavate, white, with larger, more irregular, sterile flowers at the base, the sterile staminate part usually ± swollen and wider than the pistillate part; flowers unisexual, naked; staminate flowers consisting of 3 or 4 stamens united into a synandrium, the synandria truncate to somewhat rounded at apex, the connective of the anthers thick, dehiscent below the apex of the connective by a short slit, rounded or obtuse at the base; pistillate flowers connate, the ovary obovoid or oblong-obovoid, normally 2-celled (rarely 3- or 1-celled); ovules 1 (rarely 2) per cell, erect, anatropous; stigmas usually discoid or bilabiate, rarely orbicular or cup-shaped; fruits baccate, connate into an ovoid syncarp, this usually brown, sometimes white at maturity; seeds obovoid or ovoid; funicle short; testa smooth, thin, black or dark brown, shiny; endosperm lacking.

KEY TO THE SECTIONS OF *SYNGONIUM*

1a. Leaf blades of adult plants simple; leaf blades of juvenile and the pre-adult climbing phases not markedly different from those of the adult.
  2a. Leaf blades lacking posterior lobes or the blades merely subcordate. .... Section *Oblongatum* (Species 1–3)
  2b. Leaf blades with large, well-developed posterior lobes, the blades ovate, oblong-ovate or hastate. .... Section *Cordatum* (Species 4–13)
1b. Leaf blades of adult plants markedly divided, trisect, 5–11-palmatisect or incised-lobate; leaf blades of juvenile and pre-adult climbing phases markedly different from those of the adult.
  3a. Leaf blades of adult plants incised-lobate (the anterior lobe pinnately lobed); leaf shape of pre-adult climbing phase usually not simple, usually variously lobed but not as deeply lobed as the adult. .... Section *Pinnatilobum* (Species 14)
  3b. Leaf blades of adult plants trisect or 5–11-pedatisect; leaf shape of pre-adult climbing phase simple, usually hastate or sagittate. .... Section *Syngonium* (Species 15–33)

KEY TO THE SPECIES OF *SYNGONIUM*

1a. Leaf blades not divided into segments.
  2a. Leaf blades oblong-elliptic or ovate-elliptic, merely rounded to subcordate at the base; petioles sheathed nearly their entire length.
    3a. Blades mostly less than 15 cm long; primary lateral veins arising from the lower half of the blade. .... 1. *S. armigerum*
    3b. Blades commonly more than 15 cm long; primary lateral veins uniformly distributed along the blade.

4a. Petioles 9–33 cm long, the sheath 2–3 cm wide (when flattened), usually extending over the base of the blade, rounded at the apex; blades 13–34 cm long; peduncle 6–8 cm long (to 10 cm long in fruit); fruiting spathe tube 8–10 cm long. ____ 2. *S. llanoense*
4b. Petioles 6–10 cm long, the sheath less than 1 cm wide (when flattened), usually ending well below the base of the blade, acute at the apex; blades 14–23 cm long; peduncle to 4 cm long (in fruit); fruiting spathe tube ca. 4 cm long. ____ 3. *S. oduberi*
2b. Leaf blades ovate to hastate or sagittate, conspicuously lobed at the base; petioles sheathed ⅓–¾ their length.
5a. Stems glaucous; juvenile blades thick, cordate; adult blades thick, the veins not prominent. ____ 4. *S. chiapense*
5b. Stems not glaucous; juvenile blades thin, often hastate or sagittate; adult blades thin, the veins prominent.
6a. Adult blades markedly hastate with pronounced, pointed, posterior lobes directed outward at ca. 45° angle, the anterior lobe somewhat constricted at the base. ____ 10. *S. hastifolium*
6b. Adult blades ovate, oblong-ovate or elliptic-hastate, not markedly hastate, the posterior lobes rounded or, if pointed, then much smaller than the anterior lobe, usually directed mostly downward, the anterior lobe usually not markedly constricted at the base (except *A. hastiferum*).
7a. Blades with the lower surface pale, matte, whitish; basal veins fusing to form a posterior rib more than 3 cm long; Costa Rica and Panama. ____ 13. *S. schottianum*
7b. Blades with the lower surface semiglossy or matte but never whitish; basal veins forming a distinct posterior rib or nearly free to the base.
8a. Blades elliptic-hastate, usually weakly or strongly constricted between the anterior and posterior lobes, the posterior lobes usually narrowly angular; Costa Rica. ____ 9. *S. hastiferum*
8b. Blades ovate or oblong-ovate, not constricted between the anterior and posterior lobes, the posterior lobes rounded or obtuse, not acutely angular; Mexico or South America and western Panama.
9a. Blades lacking a well-developed posterior rib (united basal vein), the posterior rib lacking or less than 1 cm long, the basal veins all or nearly all submarginal to the sinus; spathe tube less than 5 cm long at anthesis.
10a. Blades broadest at the base or in the lower third; primary lateral veins 5–9 pairs, unbranched; tertiary veins distinct, irregular and wavy, relatively remote from one another; western Venezuela. ____ 11. *S. meridense*
10b. Blades broadest at about the middle; primary lateral veins 9–15 pairs, with distinct branches at least in the lower part of the blade; tertiary veins obscure, regular and closely parallel; northern Colombia (Chocó). ____ 5. *S. chocoanum*
9b. Blades with a well-developed posterior rib usually more than 1 cm long, the posterior rib naked for some distance from the apex of the sinus; spathe tube usually 6.5–15 cm long at anthesis; northern South America or Mexico.
11a. Blades less than 35 cm long; primary lateral veins in 3 or 4 pairs; spadix less than 8 mm diam. at the broadest point; northern Colombia (Chocó). ____ 8. *S. foreroanum*
11b. Blades mostly more than 35 cm long; primary lateral veins in 9–13 pairs; spadix 1–2.5 cm diam. at the broadest point.
12a. Spathe blade long-acuminate at the apex; northern Oaxaca (Mexico). ____ 12. *S. sagittatum*
12b. Spathe acute or short-acuminate at the apex; Colombia, Ecuador and Venezuela.
13a. Blades dark green, thin (drying blackened and papyraceous); primary lateral veins red, in moderately deep valleys; tertiary veins distinct on drying; spathe tube elliptic, light orange-red, conspicuously constricted at the apex, the blade light orange-red throughout. ____ 7. *S. dodsonianum*
13b. Blades subcoriaceous, light green, drying chartaceous, greenish brown; primary lateral veins green, not markedly sunken in valleys; tertiary veins moderately obscure on drying; spathe tube oblong-elliptic, medium green, only moderately constricted at the apex, the blade creamy white throughout. ____ 6. *S. crassifolium*
1b. Leaf blades either trilobed, trisect, 5–11-pedatisect or incised-lobate.
14a. Blades incised-lobate; Guatemala and Mexico. ____ 14. *S. steyermarkii*
14b. Blades trilobed, trisect or 5–11-pedatisect.
15a. Spathe tube cylindroid, frequently more than 6 cm long; spathe blade usually twice as long as the staminate part of the spadix; fruiting spadix elongate, ± cylindroid; West Indies. ____ 17. *S. auritum*
15b. Spathe tube usually ellipsoid or ovoid (oblong-ovoid in *S. atrovirens*), rarely more than 6 cm long (to 8 cm in *S. neglectum*, to 7 cm in *S. atrovirens* and *S. chiapense*); spathe blade usually only slightly longer than the staminate part of the spadix; fruiting spadix ± ellipsoid; Central and South America and Trinidad.

16a. Adult blades trisect or trilobed, sometimes appearing almost 5-parted because of conspicuous auricles on lateral segments.
17a. Blades with the lateral segments merely inequilateral, not markedly auriculate *or* if markedly auriculate, the auricle at least not pinched off to appear like another segment.
18a. Median lobe of the adult blade with the primary lateral veins departing the midrib at almost 90° angle (rarely at less than 65° angle).
19a. Lateral leaflets scarcely unequal at the base, not at all auriculate; Ecuador on the Atlantic slope. ---------------------------------- 29. *S. sparreorum*
19b. Lateral leaflets noticeably unequal at the base, sometimes ± auriculate; Central and South America.
20a. Primary lateral veins of the median leaflet indistinct, scarcely more prominent than the lesser veins; Costa Rica and Panama. -- 23. *S. laterinervium*
20b. Primary lateral veins of the median leaflet distinct, much more prominent than the lesser veins; South America.
21a. Spathe tube narrowly oblong-ovoid, 5.5–7.2 cm long, scarcely constricted at the apex; western Venezuela. ---- 16. *S. atrovirens*
21b. Spathe tube oblong-elliptic, 3–3.5 cm long, conspicuously constricted at the apex; western Amazon Basin, Brazil, Peru and Bolivia. -------------------------------------- 33. *S. yurimaguense*
18b. Median lobe of the blade with the primary lateral veins in the lower third of the leaflet sharply ascending, departing the midrib at usually less than 60° angle.
22a. Lateral segments of the adult blade with a conspicuous, usually ± hastate auricle.
23a. Young leaves, peduncle and spathe tube pruinose; leaves 30–45 cm wide; highland species occurring in wet forest at elevations above 1300 m in Chiriquí (western Panama) and Costa Rica. -- 20. *S. glaucopetiolatum*
23b. Young leaves, peduncle and spathe tube not pruinose; leaf blades less than 25 cm wide (rarely to 35 cm wide in *S. salvadorense*); principally lowland species occurring below 700 m, primarily in tropical forest on the Pacific slope from Chiapas, Mexico, and Guatemala to Panama.
24a. Peduncle 9–18 cm long (to 25 cm long in fruit); leaf blades with 3–5 primary lateral veins on each side, these mostly restricted to the lower half of the blade; stems usually pruinose; southern Mexico to El Salvador. ---------------------- 28. *S. salvadorense*
24b. Peduncle 3.5–9 cm long; leaf blades with 6 or more primary lateral veins on each side, ± equally distributed throughout the blade; stems not pruinose; Costa Rica and Panama. -- 25. *S. mauroanum*
22b. Lateral segments not prominently auriculate or, if auriculate, the auricle at least not at all hastate.
25a. Leaf blades merely trilobed with the segments markedly confluent *and* less than 12 cm long (confluent in *S. chiapense* and *S. podophyllum* but these have a median lobe more than 16 cm long); rare species from Ecuador. ---------------------------- 21. *S. harlingianum*
25b. Leaf blades with usually 3 distinct leaflets (except *S. chiapense*, usually unlobed, and sometimes *S. podophyllum*.
26a. Lateral segments with the auricles moderately conspicuous and directed downward, more or less in line with the midrib of the segment; stems, petioles and peduncles glaucous or the segments silky due to conspicuous papillae on the upper surface; spathe tube dark red inside.
27a. Stems, petioles and peduncles glaucous; blades not silky pubescent due to papillae on the surface. 22. *S. hoffmannii*
27b. Stems, petioles and peduncles not glaucous; blades silky on the upper surface due to papillae. ---- 32. *S. wendlandii*
26b. Lateral segments with auricles conspicuous or not, but usually not directed downward more or less in line with the midrib of the segment; plants lacking silky upper blade surfaces; plants usually not glaucous or if glaucous, the lateral segments definitely lacking conspicuous auricles, spathe tube variously colored within.
28a. Lateral leaflets narrowly acute to attenuate at the base, not the least auriculate.
29a. Inflorescence solitary; stems less than 1 cm diam., densely and minutely papillate; below 500 m, Honduras to Costa Rica. ------------ 30. *S. standleyanum*

29b. Inflorescences paired; stems ca. 2 cm diam., smooth; above 1000 m elevation, Peru. ---------- 19. *S. gentryanum*

28b. Lateral leaflets usually conspicuously inequilateral and auriculate (or at least with the outer margin broadly rounded).

30a. Leaf blades thin, the veins conspicuously sunken (when fresh).

31a. Median leaflet with 5–9 pairs of primary lateral veins, drying greenish brown; juvenile blades sagittate; inflorescences 1 or 2 per axil; tropical moist and premontane moist forest, Costa Rica and Panama. ---- 25. *S. mauroanum*

31b. Median leaflet with 10–16 pairs of primary lateral veins, drying black; juvenile blades elliptic; inflorescences 1–5 per axil; tropical wet and premontane wet forest, Honduras to Panama. ---------- 31. *S. triphyllum*

30b. Leaf blades moderately thick to coriaceous, the veins not conspicuously sunken.

32a. Blades mostly less than 20 cm long, the lateral leaflets mostly narrowly rounded at the apex; juvenile leaves purplish violet on the lower surface; adult blades and stems drying conspicuously brown; tropical moist and premontane wet forest, central Panama. ---------- 18. *S. erythrophyllum*

32b. Blades mostly more than 20 cm long (sometimes less in *S. standleyanum* and *S. mauroanum*), the lateral leaflets usually acute at the apex; juvenile leaves green beneath; adult blades and stems drying mostly green to black (the stems sometimes drying brown).

33a. Peduncles 1–3 per axil, usually more than 9 cm long, frequently 14–25 cm long in fruit.

34a. Juvenile blades broadly ovate-cordate; adult blades thick, the median segments 28–52 cm long, the lateral segments smaller (10–20 cm long), directed nearly backwards; peduncle and spathe tube blue glaucous; Mexico (Chiapas, mostly eastern, and southern Veracruz). ---------- 4. *S. chiapense*

34b. Juvenile blades hastate or sagittate; adult blades thin, the median lobe less than 28 cm long, the lateral segments not markedly smaller, mostly directed forward; peduncle and spathe tube green; southwestern Mexico (Chiapas) and western Guatemala to Costa Rica. ---------- 28. *S. salvadorense*

33b. Peduncles 4–11 per axil, usually less than 9 cm long, to 13 cm long in fruit. ---- 27a. *S. podophyllum* var. *podophyllum*

17b. Blades with the lateral segments bearing conspicuous auricles, these pinched off to appear like separate segments (some leaf blades of *S. triphyllum* with the lateral segments not pinched off).

35a. Stems with large, elongate projections. ---- 27b. *S. podophyllum* var. *peliocladum*

35b. Stems lacking elongate projections.

36a. Upper blade surface silky due to papillae; Costa Rica. ---- 32. *S. wendlandii*

36b. Upper blade surface lacking papillae.

37a. Median leaflet with 10–16 pairs of prominently sunken primary lateral veins; spathe tube red inside. ---------- 31. *S. triphyllum*

37b. Median leaflets with usually fewer than 8 pairs of primary lateral veins, these not conspicuously sunken; spathe tube green or red to violet purple inside.

38a. Spathe tube red to violet purple inside; inflorescences 1–4 per

axil, usually no more than 3; blades usually drying black; tropical wet, premontane wet or more commonly lower montane rainforest, Costa Rica to Panama. .... 22. *S. hoffmannii*

38b. Spathe tube green inside; inflorescences 4–11 per axil; blades usually drying green.

39a. Stems not glaucous, sometimes with numerous rough emergences; leaf segments usually slender, of nearly equal size and shape; petioles subterete, usually with a sharp medial rib; rachis usually gradually curved, not angular between each segment; staminate flowers deeply retuse at the apex, showing no indication of the line of fusion; Mexico to Costa Rica. .... 15. *S. angustatum*

39b. Stems glaucous (at least in northern Central America), smooth, lacking any emergences; leaf segments usually somewhat unequal, not of relatively uniform size and shape; petioles subterete or with only an obtuse medial rib; staminate flowers truncate at the apex with an indication of the line of fusion; Mexico to Panama. .... 27a. *S. podophyllum* var. *podophyllum*

16b. Adult blades either 5–11-pedatisect or incised lobate (i.e., the segments of the anterior lobe pinnate).

40a. Stems with conspicuous, elongate, projections; sea level to 1000 m, Costa Rica and Panama on the Atlantic slope (Alajuela to Bocas del Toro). .... 27b. *S. podophyllum* var. *peliocladum*

40b. Stems lacking conspicuous, elongate projections; geographical ranges various.

41a. Peduncles usually 1 (sometimes 2 or 3); entire inflorescence usually 20–40 cm long (or in *S. mauroanum* less than 20 cm long with the leaf blades thin and with many sunken veins); spathe tube not glaucous; staminate part of the spadix 8.5–14 cm long (or less in *S. mauroanum*); Mexico, Costa Rica and Panama.

42a. Inflorescence less than 20 cm long; staminate part of the spadix less than 8 cm long; stems less than 1.5 cm diam.; premontane moist forest, western Panama and Costa Rica. .... 25. *S. mauroanum*

42b. Inflorescence usually more than 20 cm long; staminate part of the spadix more than 8 cm long; stems more than 1.5 cm diam.; blades chartaceous, the veins not sunken; not occurring in premontane moist forest, Mexico. .... 26. *S. neglectum*

41b. Peduncles usually numerous (unless collected when flowers are first beginning to develop); entire inflorescence usually less than 20 cm long; spathe tube often glaucous; staminate part of spadix 2.5–9 cm long; Mexico to Ecuador, Brazil and Bolivia.

43a. Adult leaf blades thick, the upper surface very smooth, the median leaflet often more than 35 cm long; juvenile blades thick, large, cordate; peduncles 10–20 cm long; spathe tube usually glaucous, even in fruit; mature infructescence usually more than 10 cm long, 5–8 cm wide. .... 24. *S. macrophyllum*

43b. Adult leaf blades thin, the upper surface not smooth, the median leaflet usually less than 35 cm long; juvenile leaves thin, sagittate or hastate (or if cordate, very small); peduncles less than 10 cm long at anthesis; spathe tube usually not glaucous in fruit; mature infructescence usually less than 10 cm long, 4.5 cm wide.

44a. Stems not glaucous, sometimes with numerous rough emergences; leaf segments usually slender, of nearly equal size and shape; petioles subterete, usually with a sharp medial rib; rachis usually gradually curved, not angular between the segments; staminate flowers deeply retuse at the apex, showing no indication of the line of fusion; Mexico to Costa Rica. .... 15. *S. angustatum*

44b. Stems glaucous (at least in northern Central America), smooth, lacking any emergences; leaf segments usually somewhat unequal, not of relatively uniform size and shape; petioles subterete or with only an obtuse medial rib; staminate flowers truncate at the apex with an indication of the line of fusion; Mexico to Panama. .... 27a. *S. podophyllum* var. *podophyllum*

A. **Syngonium** section **Oblongatum** Croat, sect. nov. TYPE SPECIES: *Syngonium llanoense* Croat.

Lamina adulta oblonga aut oblonga-elliptica, basi subcordata; petiolus vaginatus prope usque ad apicem; lamina juvenalis intermediaque laminae adultae similis.

1. Syngonium armigerum (Standley & L. O. Williams) Croat, comb. nov.

Philodendron armigerum Standley & L. O. Williams, Ceiba 3:107. 1952. TYPE: Costa Rica, Cartago, on hills near Moravia (SE of Turrialba) on road past Tuis, 1300 m, *L. O. Williams 16170* (EAP, holotype; US, isotype). NOTE: The original description gave Limón Province as the location. However, Moravia is considerably to the west of the Limón border.

Scandent hemiepiphyte; stems 5–6 mm diam., drying brown with longitudinal wrinkles; internodes 2–4 cm long; leaves persisting at all nodes at least in the upper 30 cm of the stem; petioles 5–7 cm long, (that of the leaf subtending the inflorescence to 10 cm long), sheathed nearly to the apex, the sheath 5–7 mm wide when flattened, emarginate at the apex; blades simple, membranous, oblong to oblong-elliptic, 8–15 cm long, 3–6 cm wide, acute to narrowly rounded at the apex, apiculate, weakly lobed at the base, the lobes broadly triangular or rounded, obtuse, the lower surface with obscure black punctations, 5–7 veined at base; primary lateral veins 5–6 pairs all arising in the basal half of the blade, ascending at a sharp angle to the margin near the apex, each forming a separate collective vein; tertiary veins distinct. *Inflorescences* usually one per axil; peduncles to 5.3 cm long, 5 mm diam. (dried); fruiting spathe coriaceous, ca. 7 cm long. *Infructescences* not seen. Fig. 1.

DISTRIBUTION: The species is known only from the type locality, which is an area of premontane wet forest or premontane rain forest.

The type collection made in April was in mature fruit.

COSTA RICA: LIMÓN: Near Moravia, *Williams 16170* (EAP, US).

2. Syngonium llanoense Croat, sp. nov. TYPE: Panama, Canal Zone, Summit Gardens (no doubt collected originally in Panamá or Colón Province), *Croat 17148* (MO-219002, holotype).

Caudex haud glaucus, ca. 2 cm diam.; foliorum petiolus 9–27 cm longus, ad apicem vaginatus; lamina oblongata-elliptica, 18–28 cm longa, 8–11 cm lata, apice acuminata, basi rotundata ad subcordata. Inflorescentia usque 2 in axilla; spathae tubus 5–6 cm longus, ca. 3 cm latus, viridis; spathae lamina e viridi alba, ca. 10 cm longa; spadix 11.5 cm longa; parte mascula spadicis ca. 9.5 cm longa, alba, parte feminea spadicis viridi, 2 cm longa, basi 9 mm diam., apice 6 mm diam. (in sicco).

Juvenile plants with trailing stems, the leaves much like those of the adult but smaller; stems medium green when young, becoming dark olive-green to purplish; internodes 3–6 cm long, to 6 mm wide, weakly sulcate above the petioles in the lower part of the internode; petioles 6 cm or longer, sheathed nearly throughout; the sheath 1–1.3 cm wide when flattened. Adult plants with stems closely appressed to trees, dark olive-green, shiny, to ca. 2 cm diam., becoming brown in age, drying with longitudinal wrinkles; internodes to 5 cm or more long on the lower parts of the stem, 1–3 cm near the apex; sap pale tan; leaves persisting on the upper 1 m or more of the stem; petioles 9–33 cm long, broadly sheathed almost throughout, broadly canaliculate from the end of the sheath to the blade, the sheath 2–3 cm wide when flattened (to 5 cm wide when subtending an inflorescence), the margins of the sheath erect at the base, broadly spreading toward the apex, free-ending and emarginate at the apex (with the apical lobes sometimes extending beyond the bottom of the blade); blades simple, oblong-elliptic to ovate-elliptic, gradually acuminate and turned down at the apex (the acumen apiculate), narrowly rounded to subcordate at the base, 13–34 cm long, 6–13 cm wide, the

Figures 1–4.—1. *Syngonium armigerum, Williams 16170*; plant bearing mature infructescence.—2. *S. llanoense, Croat 17148*; base of blade with free-ending petiole sheath (new leaf emerging from sheath) ($\times^1/_3$).—3. *S. llanoense, Croat 36946*; plant bearing young infructescences ($\times^1/_{10}$).—4. *S. llanoense, Croat 17148*; base of lower surface of blade showing petiole sheath ($\times^5/_7$).

posterior lobes 1–2 cm long, held almost erect, rounded at the apex, the upper surface medium green, matte to semiglossy, the lower surface much paler, matte; midrib prominently sunken; primary lateral veins 10–18 pairs, sunken above, raised beneath; interprimary veins few; tertiary veins distinctly visible; principal collective vein weakly sunken, 4–8 mm from the margin, weakly loop-connected between the primary veins. *Inflorescences* usually 2 per axil, erect at anthesis; prophylls ca. 20 cm long; peduncles 6–8 cm long, the epidermis in part becoming inflated on drying; spathe tube green, ovoid-ellipsoid, 5–6 cm long, ca. 3 cm diam.; spathe blade greenish-white, ca. 10 cm long, acuminate at the apex; spadix 11.5 cm long (on dried plants); pistillate portion of the spadix green, ca. 2 cm long, ca. 9 mm diam. at the base, ca. 6 mm diam. at the apex; staminate and sterile portions of the spadix 9.5 cm long, white, the sterile staminate portion ca. 12 mm diam., the staminate flowers mostly ca. 2 mm diam., the sterile flowers mostly 4–5 mm diam. *Infructescences* pendent; peduncles green, weakly flattened, to 10 cm long, fruiting spathe oblong-elliptic, 8–10 cm long, 3–4.5 cm diam., fruiting spadix subglobose, ca. 5 cm long, 4 cm diam., tan cream; seeds subglobose, ca. 8 mm diam. Figs. 2–4, 21.

DISTRIBUTION: *Syngonium llanoense* was first collected at Summit Garden but later discovered in both Panamá and Colón provinces in areas adjacent to the Canal Zone. It occurs naturally only in tropical wet forest life zones.

The species is unique among known members of the genus in having oblong-elliptic leaves. Another distinguishing feature is the petiole which is sheathed throughout its length.

Flowering inflorescences have been seen in June and fruits have been found in June, July, and October.

PANAMA: CANAL ZONE: Summit Gardens, *Croat 10831* (DUKE, MO, SCZ), *17148, 35999* (MO). COLÓN: Río Guanche, *Croat 36946* (MO); Vicinity of Río Indio, *Croat 33636A* (MO). PANAMÁ: El Llano-Cartí Road, *Croat 25148, 34764, Kennedy 1785* (MO).

3. **Syngonium oduberi** Ray, Aroideana 3:128. 1980. TYPE: Costa Rica, Osa Peninsula, Corcovado National Park, *Ray 4* (GH, holotype).

Juvenile plants with trailing stems; internodes 4–7 mm long, 3 mm wide; leaves much like those of the adult but smaller and narrower; petioles 4.5–5.5 cm long; blades 13–15 cm long, 3.5–4.5 cm wide. Adult plants with stems closely appressed to trees; internodes 1–2 cm long, ca. 6 mm wide; petioles 6–10 cm long, sheathed throughout except for the apical 0.5–1 cm, the sheath free-ending and apiculate at the apex, not extending beyond the base of the blade, the apical part flattened adaxially with a medial rib, the margins acute; blades simple, oblong-elliptic, gradually acuminate at the apex, slightly constricted above the posterior lobes (less so on juvenile blades), 14–23 cm long, 6–8 cm wide, the posterior lobes bluntly acute, 8–13 mm long; primary lateral veins 12–14 on each side, sunken above, raised beneath; tertiary veins prominent; latex not milky though slightly orange in mature stems. *Infructescences* pendent; peduncles 3.5 cm long; fruiting spadix 4 cm long, 2.5 cm diam. The flowering spadix has not been seen; a nearly mature fruit was collected in July. Figs. 13–14.

DISTRIBUTION: *Syngonium oduberi* has been collected only once, in wet forest, at ca. 100 m elevation.

The species is distinguished by its oblong-elliptic leaves and almost fully sheathed petioles. It is most closely related to *S. llanoense* from the isthmus of Panama. It is distinguished from that species in having smaller leaves and stems, in having the posterior lobes bluntly acute (versus rounded in *S. llanoense*) and in having the sheath end well below the blade. In *S. llanoense* the sheath generally extends beyond the base of the blade.

COSTA RICA: PUNTARENAS: Parque Corcovado, Osa Peninsula, near Llorana, 100 m, *Ray 4* (GH).

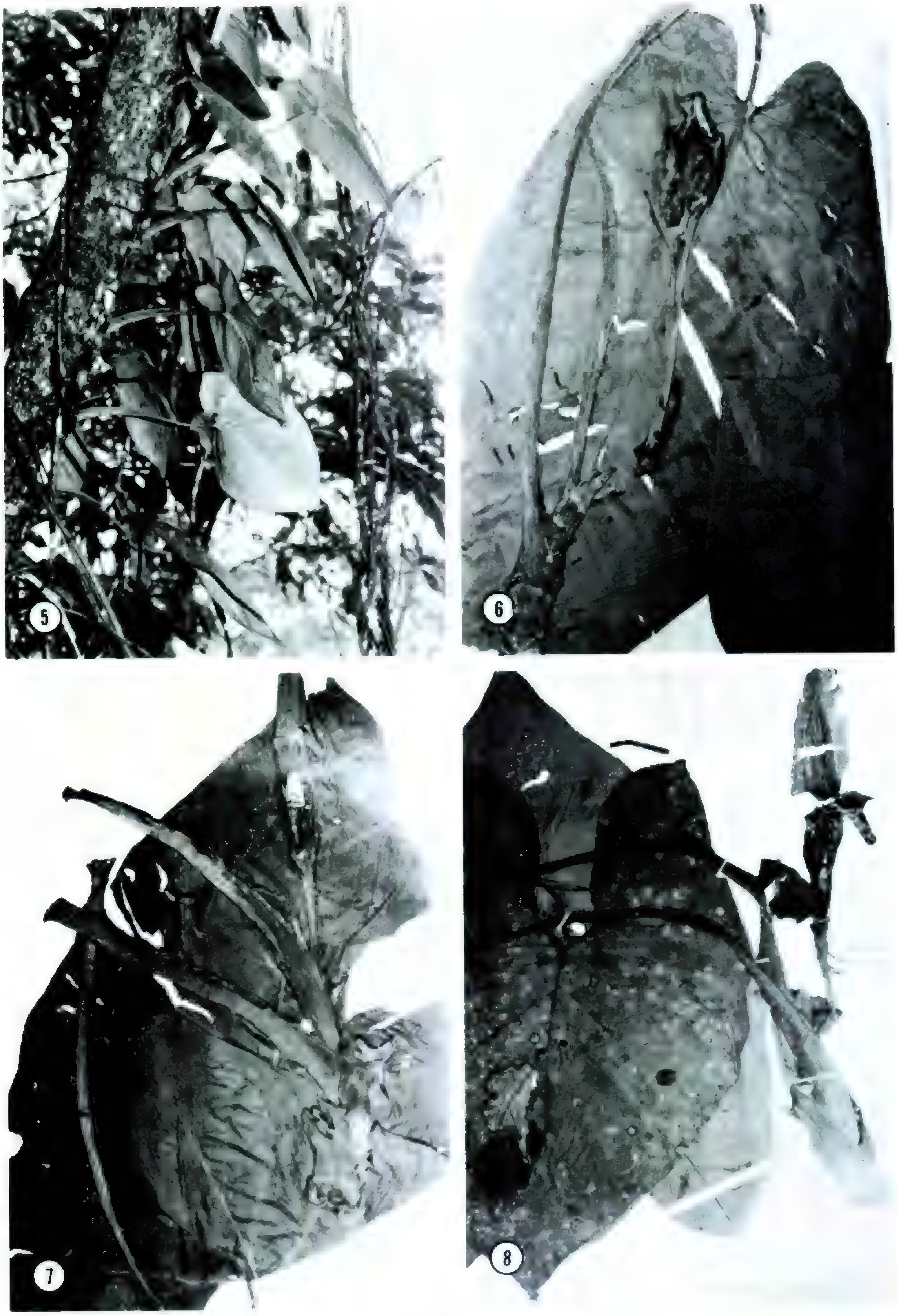
B. Syngonium section **Cordatum** Croat, sect. nov. TYPE SPECIES: *Syngonium schottianum* Wendl.

Lamina adulta simplex, lobis posticis bene evolutis; petiolus e $^{1}/_{2}$ ad $^{4}/_{5}$ longitudinis usque vaginatus; lamina juvenalis intermediaque laminae adultae similis.

4. Syngonium chiapense Matuda, Revista Soc. Mex. Hist. Nat. 11:94–95. 1950. TYPE: Mexico, Chiapas, Piedra de Huixtla, *Matuda 18619* (MEXU, holotype; DS, isotype).

S. llamasii Matuda, Cact. & Sucul. Mexico 2:79, *fig. 52.* 1957. TYPE: Mexico, Chiapas, El Suspiro, near Ocozocuautla, 600 m, *Matuda 32637* (MEXU, holotype).

Juvenile plants with glaucous stems; internodes 5–23 cm long, less than 1 cm wide; petioles sheathed ½–¾ their length, blades ovate-cordate, 9–30 cm long, 5–17 cm wide, acuminate at the apex. Adult plants with stems green, usually glaucous; internodes 12–20 cm long, becoming closer at the apex, 2–6 cm long, 2.5–4 cm diam.; petioles 30–60 cm long, sheathed about $^{4}/_{5}$ their length, subterete above the sheath, weakly flattened on the upper surface; blades with the upper surface matte, seldom weakly glossy, the lower surface matte, much paler, ovate-cordate to 3-lobed, abruptly acuminate to obtuse-mucronate at the apex, the entire blade with the anterior lobe 28–65 cm long, 18–35 cm wide, broadest at about the middle, only slightly or not at all constricted at the base, the posterior lobes rounded or subhastate, the sinus very narrow or open and broader than deep, the posterior rib sometimes naked 5–20 mm; 3-lobed blades with the anterior lobe broadly ovate, 28–52 cm long, abruptly constricted at the base and confluent with the posterior lobes, the latter ovate to obovate, 10–20 cm long, directed backwards or at ca. 90° angle to the anterior lobe, acute to narrowly rounded at the apex, bluntly auriculate at the base on the lower side; primary lateral veins mostly 5–8(–10) pairs, slightly sunken; the primary lateral veins convexly raised, the tertiary veins clearly visible. *Inflorescences* 1–3; peduncles to ca. 10 cm long and erect at anthesis, green and glaucous, 12–18 cm long and pendent in fruit; spathe tube ellipsoid to oblong-ovoid or cylindroid, greenish outside, glaucous, 5–7 cm long, to 3 cm diam. inside, yellowish white at the base, purplish at the apex; spathe blade broadly elliptic, white, shortly cuspidate at the apex, 5–9 cm long, 5–7 cm wide; pistillate portion of the spadix 3–4 cm long, the ovary ca. 5 mm long, 3 mm wide; staminate portion of the spadix ca. 5–9 cm long, to 1.5 cm diam., the staminate flowers ca. 3 mm long, the anthers 4, cross-



FIGURES 5–8.—5. *Syngonium chiapense, Croat 48016*; adult plant (×1/20).—6. *S. chocoanum, Forero et al. 3324*; adult blade with infructescence.—7. *S. dodsonianum, Dodson & Gentry 10063*; adult blade and inflorescence (×1/3).—8. *S. foreroanum, Forero et al. 3385*; adult blade and inflorescence (×1/4).

shaped. *Infructescences* usually rather massive, bluish glaucous, ± ellipsoid, ca. 8–10 cm long, 4.5–5 cm diam. Figs. 5, 22.

DISTRIBUTION: *Syngonium chiapense* is known for certain only from southern Mexico (Oaxaca and southern Veracruz), but a sterile collection from Guatemala (Baja Verapaz) also appears to be this species. The species occurs only on the Atlantic coast from sea level to more than 1200 m but most commonly occurs above 350 m in life zones ranging from tropical moist forest through tropical wet forest.

Syngonium chiapense is perhaps most closely related to *S. macrophyllum*. The two species have nearly identical juvenile leaves and both have glaucous stems and inflorescences in Mexico. The adult foliage of *S. macrophyllum* with 7–9 free leaflets is never confused with this species which is commonly entire or with merely a single pair of confluent posterior lobes.

Fruits have been seen July–September.

GUATEMALA: BAJA VERAPAZ: S of Purulha, *Croat 41218* (MO).

MEXICO: CHIAPAS: Comaltitlán, *Matuda 17882* (MEXU); N of Ocozocoautla, *Croat 40662* (MO); Piedra de Huixtla, *Matuda 18619* (DS, MEXU). OAXACA: Vicinity of Valle Nacional, *Croat 39720, 39754, 39805, 43913* (MO), *48016* (CAS, MO, MEXU), *Moore & Bunting 8895* (BH, MO). VERACRUZ: E of Coatzacoalcos, *Croat 40060* (MO); S of Catemaco, *Moore & Bunting 8926* (MO), *8938* (BH, MO).

5. **Syngonium chocoanum** Croat, sp. nov. TYPE: Colombia, Chocó, Municipio of Nóvita, slope N of Cerro Torrá Filo ridge E of Río Surama, along trail to Alto del Oso, 500–600 m, *Forero, Gentry, Sugden & Daly 3324* (COL, holotype; MO-2604930, isotype).

Planta hemiepiphytica; caudex ca. 2 cm diam., internodiis brevibus; lamina simplex; petiolus usque 5–6 cm e apice vaginatus; lamina anguste ovata, basi cordata; folia venis lateralibus utroque latere 9–15, infimis ramosis; venis tertiariis tenuibus, approximatis, obscuris. Inflorescentia ignota; spatha fructifer viridis, oblonga-elliptica, 8 cm longa.

Hemiepiphytic creeper; stems ca. 2 cm diam.; internodes short, those on the upper part of the stem ca. 1 cm long; cataphylls thin, ca. 19 cm long, ca. 1 cm wide; petioles to 43 cm long, narrowly sheathed to within 5 cm of the apex, the margins of the sheath to 1 cm high, markedly broadened within 6 cm of the base, acute and free-ending at the apex (the free part ca. 1.5 cm long, the unsheathed part of the petiole ca. 3 mm diam. (dried); blades entire, moderately thin, narrowly ovate, acute or bluntly acuminate at the apex, narrowed and cordate at the base, 26–36 cm long, 14–23 cm wide, the posterior lobes narrowly rounded; primary lateral veins 9–15 pairs, arising at ca. 45–50° angle, straight or weakly curved to the collective vein, with prominent branches (especially in the lower half of the blade) these curved and closely paralleling the primary lateral veins; tertiary veins obscure (at least on drying), close, markedly parallel; collective veins 3, obscure, the first ca. 5 mm from the margin; basal veins 4 or 5 pairs, the lowermost 3–4 basal veins coalesced ca. 5 mm before the base. *Inflorescences* solitary(?); flowering spathe not seen. *Infructescences* with the peduncles to 11 cm long, 6 mm diam. (dried) midway, smooth, fruiting spathe tube narrowly elliptic, green, 8 cm long, 4 cm diam.; syncarp oblong-elliptic, 5.5 cm long, 4 cm diam., tan. Fig. 6.

DISTRIBUTION: *Syngonium chocoanum* is known only from the southern part of the Chocó Department, Colombia, in tropical wet forest.

It is apparently related to both *S. hastiferum* from Costa Rica and *S. meridense* from western Venezuela, differing from both in having fine, closely parallel tertiary veins. It differs from *S. hastiferum* in having an open sinus with rounded posterior lobes. It differs from *S. meridense* in having a narrower sinus (versus broad and open in *S. meridense*). In respect to the sinus alone *S. chocoanum* lies intermediate between *S. hastiferum* and *S. meridense*, but the very different venation is sufficient to distinguish the species.

COLOMBIA: CHOCÓ: Municipio de Nóvita, N of Cerro Torrá Filo, *Forero et al. 3324* (COL, MO); Valley of Río San Juan, Quebrada La Sierpe, *Forero et al. 3965* (COL, MO).

6. **Syngonium crassifolium** (Engler) Croat, comb. nov.

Porphyrospatha crassifolia Engler, Bot. Jahrb. Syst. 37:140. 1905. TYPE: Colombia, Antioquia, am Riachon über Amalfi, 1800 m, *Lehmann* (Sept. 1884) (B, holotype).

Juvenile plants with scandent stems; internodes 10–20 cm or more long, ca. 1 cm diam., petioles sheathed to beyond the middle; intermediate stems climbing; petioles 15–20 cm long, sheathed ca. ⅔ their length; juvenile blades simple, ovate-oblong, abruptly acuminate at the apex, weakly hastate at the base, 15–25 cm long, 8–13 cm wide, the anterior lobe weakly constricted at the base, the posterior lobes 4–8 cm long, narrowly rounded to acute at the apex. Adult plants epiphytic or hemiepiphytic, stem to 1 m or more long, 4–6 cm diam.; internodes to 10 cm long, much shorter near the apex, yellowish brown on drying; petioles 45–70 cm long, sheathed ¾ their length, the upper part weakly flattened adaxially near the base of the blade, becoming obtusely 1-ribbed toward the sheath, the sheath free at the apex; blades entire, ovate-hastate, abruptly acuminate at the apex, conspicuously lobed at the base, 35–70 cm long, 23–40 cm wide, the anterior lobe with the sides broadly rounded, sometimes weakly constricted at the base, the posterior lobes directed outward at ca. 45° angle, 15–25 cm long, usually narrowly rounded at the apex, the sinus 6–15 cm deep, usually narrow, sometimes as broad as deep, the lower surface slightly paler than the upper surface; primary lateral veins 10–13 pairs, joining the midrib at ca. 30° angle, sunken on the upper surface, raised on the lower surface; reticulate veins obscurely visible on the upper surface, clearly visible beneath; posterior rib prominently raised, extending straight to the apex of the posterior lobes, naked 2–3 cm; primary collective vein less than 1 cm from the margin. *Inflorescences* several, erect; peduncles 8–15 cm long; spathe tube pale green, to 7 cm long, bluntly ribbed adaxially; spathe blade creamy white, oblong-elliptic, 9–11 cm long, constricted at the base and articulating along an elevated ring well above the end of the pistillate part of the spadix; spadix ca. 12 cm long; pistillate portion of the spadix grayish, 2–3 cm long, ca. 1 cm diam.; staminate portion of the spadix creamy white, 8–10.5 cm long, slightly narrower toward the apex, ca. 1.5 cm diam. midway, the synandrium regularly 4-lobed and truncate at the apex, weakly incised between the anthers. *Infructescences* pendent, yellowish, to ca. 9 cm long and 4.5 cm diam. Figs. 23, 24.

Distribution: The species is known from Colombia and Ecuador on the Pacific slope and in Venezuela in the state of Mérida.

The species has been collected in flower from June through October and mature fruits have been seen in late October.

Colombia: antioquia: (Photo) *Lehmann 12300* (B, MO, US).

Ecuador: cotopaxi: Santo Domingo de Los Colorados, *Ellenberg 3063* (MO). los ríos: Biological Station at Río Palenque, *Croat 38661, 38678, 38700* (MO), *Dodson 5538* (SEL, US), *Gentry 6582, 11997* (MO).

Venezuela: mérida: Between El Vigía and El Quince, *Bunting 2403* (MY).

7. **Syngonium dodsonianum** Croat, sp. nov. type: Ecuador, Los Ríos, Río Palenque Biological Station, km 56 along the road between Santo Domingo and Quevedo, 150–200 m, *Dodson & Gentry 10063* (MO-2742909, holotype; SEL, isotype).

Planta hemiepiphytica; caudex ca. 2.5 cm diam., internodiis apice 1–2 cm diam., 1–2 cm longis; lamina simplex, tenuis, atrovirida; venis lateralibus utroque latere 10–13, rubris, in vallibus; venis tertiariis distinctis in sicco. Inflorescentia solitaria?; spathae tubus ellipticus, pallide aurantiacus, apice constrictus; spathae lamina pallide aurantiaca.

Hemiepiphytic creeper; stems 2.5 cm diam.; internodes 1–2 cm long near the apex, drying brown with close longitudinal wrinkles; petioles 45–73 cm long, sheathed ca. ⅔ their length, the upper part subterete, the sheath 8–10 cm high, free-ending at the apex; blades simple, ovate, acute to abruptly acuminate at the apex, conspicuously lobed at the base, 42–53 cm long, 23–31 cm wide, thin, dark green (drying dark olive green, papyraceous), the anterior lobe 30–35 cm long, not at all constricted toward the base, the posterior lobes directed downward or slightly inward, acutely rounded at the apex, sometimes unequal, sometimes weakly constricted near the apex; midrib flat at the base, becoming weakly sunken toward the apex (at least on drying); primary lateral veins 10–13 pairs, reddish, in deep valleys; tertiary veins fine, close, distinct (at least on drying); basal veins 3–5 pairs, 3 of them coalesced 3–5 cm; posterior rib naked 2.5–3 cm, directed straight to the tip of the posterior lobe; primary collective vein 3–8 mm from the margin, weakly loop-connecting the primary lateral veins. *Inflorescences* solitary(?); peduncles ca. 9 cm long, 5–8 mm diam. (dried); spathe ca. 15 cm long; spathe tube ovoid-oblong to oblong-elliptic, 6.5–7.5 cm long, orange red, prominently constricted at the apex; spathe blade light orange red to yellow orange with reddish veins, acuminate at the apex; spadix ca. 11.5 cm long; pistillate portion of the spadix grayish, 2–2.5 cm long, 6–10 mm diam. on drying, weakly constricted at the apex, ca. 2 mm long, 1–1.5 mm diam.; staminate portion of the spadix creamy white, the sterile staminate portion ca. 2 cm long, constricted gradually toward the apex, drying 2–3 mm long, 1.5–3 mm diam., the sterile staminate portion broadest in the lower ⅓, gradually tapered to the apex, drying ca. 1.3 cm diam., the flowers more or less trapezoidal, the margins weakly crenate, the apex weakly depressed medially with no sign of fusion of the anthers. *Infructescences* not known. Fig. 7.

Distribution: *Syngonium dodsonianum* is known only from the type locality at the Río Palenque Biological Station, a region of tropical wet forest at 150–220 m in western Ecuador. It is to be expected throughout the band of wet forest in western Ecuador and perhaps also in Colombia.

FIGURES 9–12.—9. *Syngonium hastiferum, Allen 5563*; adult blade and inflorescence (×1/7).—10. *S. hastiferum, Allen 5563*; inflorescence and young infructescences.—11. *S. hastifolium, Ule 6010*; adult blades and inflorescences (×1/4).—12. *S. meridense, Bunting 4381*; adult blade with young infructescence (×1/4).

The species is most closely related to *S. crassifolium* with which it is sympatric. It differs from that species by the characters outlined in the key.

Flowering collections have been made during March and September.

ECUADOR: LOS RÍOS: Río Palenque Biological Station, *Dodson & Gentry 10063* (MO, SEL).

8. Syngonium foreroanum Croat, sp. nov. TYPE: Colombia, Chocó, Municipio of San José del Palmar, on a hill SW of the village, 1300 m, *Forero, Gentry, Sugden & Daly 3385* (COL-96613, holotype).

Planta hemiepiphytica; petiolus 45–47 cm longus, usque ad ⅓ longitudinis vaginatus; lamina tenuis, ovata, apice acuminata, lobo antico 17.5–20 cm longo, lobi posticis 10.5–15 cm longis, apice acutis obtuse, sinu basali apice obtuso aut rotundato; venis basalibus ad marginem confluentibus 1.2–1.5 cm; folia venis lateralibus utroque latere 3–4. Inflorescentia solitaria?; pedunculus 11–12 cm longus; spathae tubus oblongus-ellipticus, 6.5 cm longus; spathae lamina 12 cm longa; spadix parte feminea 2 cm longa, fusiformi, parte masculina 7 mm diam., apice acuta.

Hemiepiphytic creeper; stems 1.5 cm diam.; upper internodes ca. 1.5 cm long or shorter; petioles 45–47 cm long, sheathed 15–17 cm at the base, the sheath ca. 2 cm high near the base, weakly free-ending and acute at the apex, the unsheathed part cylindrical, ca. 4 mm diam. on drying; blades entire, ovate, abruptly acuminate or bluntly acute at the apex, deeply lobed at the base, 28–31 cm long, 19–21 cm wide, drying chartaceous, matte, the anterior lobe 17.5–20 cm long; the posterior lobes 10.5–15 cm long, directed somewhat outward, bluntly acute at the apex; sinus rounded at the apex, 2.5–3.5 cm wide; primary lateral veins 3–4 per side, arising from the midrib at 35–55° angle, weakly curved to the collective vein; secondary and tertiary veins distinct, flat; primary collective vein 2–4 mm from the margin, moderately straight, basal veins usually 3, the posterior rib straight to the tip of the posterior lobes, naked 12–15 mm at the base. *Inflorescences* solitary (?); peduncles 11–12 cm long, ca. 4 mm diam. (dried); spathe ca. 15 cm long; spathe tube ca. 6.5 cm long, ca. 1.6 cm diam., greenish; spathe blade 4 cm wide, acuminate (?) at the apex, moderately thin, at least sometimes weakly purplish-spotted throughout; spadix slender, 12 cm long; pistillate portion of the spadix fusiform, ca. 2 cm long, 7 mm diam.; sterile staminate portion of the spadix conspicuously constricted at the base, ca. 2.5 cm long, gradually broadened onto the fertile portion, the sterile staminate flowers broadest in the direction of the axis, the apex 3–3.5 mm long, 1.5 mm broad, the fertile staminate portion ca. 7.5 cm long, 7 mm diam., narrowly acute at the apex, the flowers 2 mm long, 1.5–2.5 mm diam., irregularly shaped, the margin irregularly scalloped. *Infructescences* unknown. Fig. 8.

DISTRIBUTION: *Syngonium foreroanum* is known for certain only from the type specimen. It was collected at 1300 m elevation in an area that is probably premontane wet forest. Another specimen collected at sea level (*Forero et al. 4367*) in the delta of the Río San Juan in southern Chocó might also be this species. It is described as an epiphyte but looks more like a *Xanthosoma*. It differs principally in having an ovate-triangular blade with narrowly acute lobes.

Syngonium foreroanum is most similar to *S. crassifolium* but differs from it by its smaller leaves, fewer primary lateral veins, and more delicate inflorescences.

COLOMBIA: CHOCÓ: S of Municipio of San José, *Forero et al. 3385* (COL).

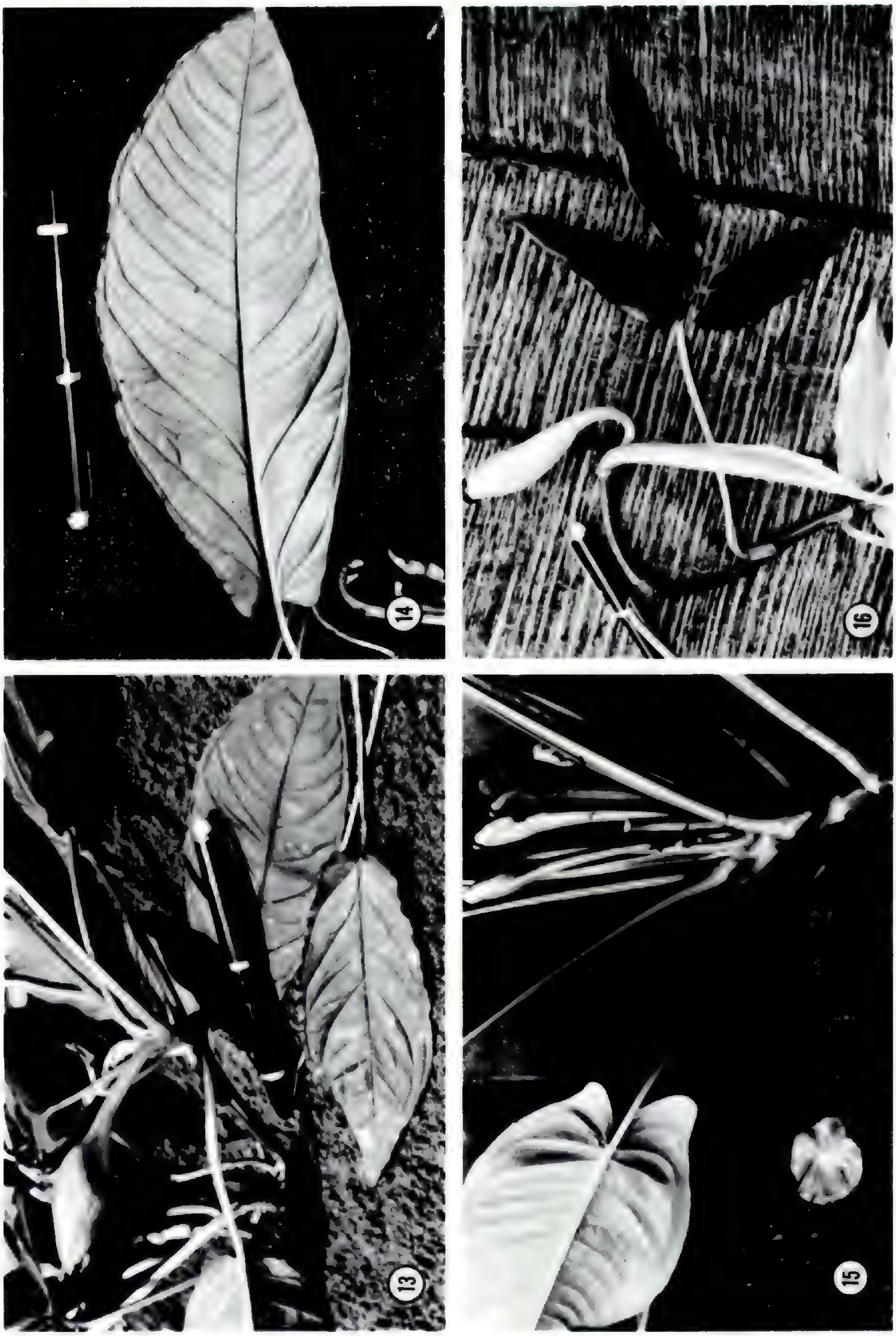
9. **Syngonium hastiferum** (Standley & L. O. Williams) Croat, comb. nov.

Philodendron hastiferum Standley & L. O. Williams, Ceiba 1:232. 1951. TYPE: Costa Rica, Puntarenas, forested hills above Esquinas, in region between Río Esquinas and Palmar Sur de Osa, *Allen 5563* (US, holotype).

Juvenile plants hemiepiphytes; stems green, not glaucous, scandent; internodes to 25 cm or more long, ca. 1 cm diam., drying brown with thin flaking epidermis; smallest leaves with the petioles sheathed almost to the apex; blades broadly ovate. Intermediate stages with petioles 20–30 cm long, sheathed to beyond the middle, the unsheathed part of the petiole terete, becoming weakly flattened laterally toward the apex; blades becoming elliptic and weakly cordate, finally with hastate lobes like the adults, then increasing only in size. Adult plants hemiepiphytic creepers; stems to 2 cm diam. (dried); internodes ca. 2.5 cm long; petioles to 37 cm long or longer, sheathed ca. $^{5}/_{6}$ their length, the sheath free-ending and emarginate at the apex; blades elliptic-hastate, triangular-acuminate at the apex, deeply lobed at the base, ca. 40 cm long, 28.5 cm wide, the anterior lobe ca. 30 cm long, gradually constricted at the base, the sides broadly rounded, the posterior lobes directed downward or slightly outward, narrowly triangular, somewhat unequal, the longer lobe to 12 cm long (from the apex of the petiole to the tip of the lobe), narrowly rounded at the apex, the shorter lobe to 8 cm long; sinus very narrow in the apical 2.5 cm, then broadly opening (when flattened), drying thin, the upper surface brown, the lower surface greenish brown; midrib flat or weakly sunken, 4 mm wide at the base; primary lateral veins ca. 13 pairs, weakly raised, the secondary and tertiary veins clearly visible; principal collective vein 8–12 mm from the margin, weakly raised on the lower surface; basal veins 3–4 pairs, the basal rib naked only within 1 cm of the end nearest the petiole. *Inflorescences* erect at anthesis, up to 5 per axil; peduncles 14–15 cm long, 5–8 mm diam. (dried); spathe tube green, 4–5 cm long, ca. 1.3 cm diam.; spathe blade greenish white, ca. 7 cm long, 2.2 cm diam. (unopened), acuminate at the apex, gradually constricted near the base; spadix sessile, white, 7.5–8.5 cm long; staminate portion of the spadix more or less ellipsoid, 5.5 cm long, 13–15 mm diam., the staminate flowers with the synandrium truncate and obscurely 4-lobed at the apex, the lobes often obscurely emarginate at the apex. *Infructescences* pendent, yellowish; not seen with mature fruit. Figs. 9, 10, 15, 25.

DISTRIBUTION: *Syngonium hastiferum* is known for certain only from Costa Rica, principally in the southeast portion in premontane wet, tropical wet and premontane rain forest life zones. A sterile juvenile collection from Darién Province, Panama, is believed to be this species also but lacks the typically narrow sinus. It is recognized by its entire leaves and relatively small lobes with narrow or often closed sinus and relatively longer lobes which are usually somewhat angular and moderately pointed at the apex. The character of rounded versus angular lobes breaks down to some extent, and plants in Costa Rican populations can be found, e.g., *Croat 32919,* which have one lobe rounded and one lobe angular.

Syngonium hastiferum is similar to *S. meridense* which has a broad sinus with



FIGURES 13–16.—13. *Syngonium oduberi*, *Ray 4*; adult blades and young infructescence (Photo by Tom Ray) ($\times 1/2$).—14. *S. oduberi*, *Ray 4*; adult blade (lower surface) (Photo by Tom Ray) ($\times 3/5$).—15. *S. hastiferum*; adult plant with young infructescences (Photo by Tom Ray) ($\times 1/7$).—16. *S. laterinervium*; adult plant with young infructescence (Photo by Tom Ray) ($\times 1/4$).

relatively short lobes that are usually rounded. The latter species is restricted to western Venezuela (Mérida). *Syngonium hastiferum* is also similar to *S. chocoanum* from Chocó of Colombia. That species differs in having an open sinus and a markedly different pattern of venation. In *S. chocoanum* the primary lateral veins have conspicuous branches and the tertiary veins are obscure, close and clearly parallel. In *S. hastiferum* the primary lateral veins have no conspicuous major branches and the tertiary veins are conspicuous, relatively remote from one another, and markedly wavy. In its venation *S. hastiferum* appears similar to *S. meridense*. *Syngonium hastiferum* is also related to *S. sagittatum* and *S. schottianum* but differs from both by its leaf shape and its smaller inflorescences. In leaf texture and color it is closer to *S. sagittatum*.

Fertile flowering collections of *S. hastiferum* have been seen in October. Immature fruits have been seen in April.

COSTA RICA: ALAJUELA: NW of Zarcero, *Croat 43579* (MO). PUNTARENAS: Between Río Esquinas and Palmar Sur de Osa, *Allen 5563* (US); Hills Above Palmar Norte, *Croat 35112* (MO); W of Rincón de Osa, *Burger & Stolze 5532* (NY); Between Palmar Sur and Piedras Blancas, *Croat 32911* (MO). SAN JOSÉ: W of San Isidro del General, *Croat 32919* (MO); SW of Río Pacuare, *Croat 35345* (MO).

10. Syngonium hastifolium Engler, Bot. Jahrb. Syst. 37:41. 1905. TYPE: Brazil, Amazonas, Río Jurua at Fortaleza, *Ule 6010* (B, holotype)

Scandent hemiepiphyte; stem thick; petiole ca. 25 cm long, sheathed more than $^3/_5$ of its length, the sheath free-ending and rounded at the apex; blade entire, acuminate at the apex, conspicuously hastate at the base, 20–25 cm long, the anterior lobe 15–18 cm long, 7.5–8.5 cm wide, constricted at the base, ca. 6.5 cm wide at the constriction, the sides broadly rounded, the posterior lobes slightly unequal, directed outward at ca. 45° angle, 10–11 cm long, 4–4.5 cm wide at their widest point, almost acute at the apex; the primary lateral veins 4–6, per side, joining the midrib at 30–45° angle; primary collective vein ca. 4 mm from the margin; posterior rib extending straight to the tip of the posterior lobe. *Inflorescences* several, erect; prophylls linear-oblong, acute at the apex, 10–15 cm long; peduncles 5–6 cm long; spathe tube oblong, ca. 4 cm long, ca. 1 cm diam.; spathe blade ovate-oblong, acute at the apex, 6–7 cm long, ca. 5 cm wide; pistillate portion of the spadix ca. 1.5 cm long, ca. 5 mm diam.; staminate portion of the spadix ca. 5 cm long, ca. 1 cm diam. (dried). *Infructescences* unknown. Fig. 11.

DISTRIBUTION: The species is known only from the type collection.

It is believed to have a close affinity with *S. podophyllum* and may merely represent an unusual, prematurely flowering individual since the leaves are virtually identical to the pre-adult leaves of that species.

The type collection was in flower in October.

For an illustration of this species see Field Museum type photo #12293.

BRAZIL: AMAZONAS: Fortaleza, *Ule 6010* [B, MO (Photo)].

11. Syngonium meridense Bunting, Acta Bot. Venez. 10:324. 1975. TYPE: Venezuela, Mérida, Caño Blanco (Puente Hierro), carretera Caño Zancudo-La Azulita, *Bunting 4381* (MY-002512, holotype; VEN, isotype).

Epiphytic or hemiepiphytic vine, usually to 2–3 m long. Juvenile plants with stems less than 1 cm diam., not glaucous; petioles 10–15 cm long, subterete above the sheath; blades oblong-elliptic, usually broadest in the middle, somewhat inequilateral, subacute to acuminate and apiculate at the apex, narrowed to a weakly lobed base; primary lateral veins 4–5 pairs, sharply ascending to the apex, each forming a distinct collective vein; posterior lobes 10–17 cm long, narrowly rounded to acutely angular. Adult plants with stems green in the apical portion, usually to 2.5 cm diam.; internodes 3–4 cm long; petioles usually 36–47 cm long, sheathed ca. ⅔ their length, the sheath open, 26–32 cm long, persistent; blades held in same plane as the petiole, thinly coriaceous, drying chartaceous, simple, subboblong-ovate to triangular-ovate, abruptly acuminate at the apex (the acumen bluntly rounded at the tip with a short apiculum), obliquely cordate at the base, 25–32 cm long, 15–21 cm wide, dark green, matte above, light green, matte below, the posterior lobes broadly rounded or rarely obtusely angular, 6–9 cm long (from the tip to the apex of the sinus), the sinus arcuate with a decurrent petiole; primary lateral veins 5–9 pairs, ascending at 40–45° angle, each forming a distinct collective vein; tertiary veins very distinct on the lower surface, almost obscure on the upper surface; basal veins 5–6 pairs, free or nearly so to the base. *Inflorescences* 2 or 3 per axil; peduncles 9–12 cm long, compressed; spathe (juvenile) 12 cm long; spathe tube fusiform, 2.5 cm long, 1.3 cm diam., dark green on the outside, pale green within; spadix (juvenile) 5 cm shorter than the spathe, subsessile; pistillate portion of the spadix 1.8 cm long, 9 mm diam. at the base, 8 mm diam. at the apex; staminate portion of the spadix somewhat clavate, 5.7 cm long, 9 mm diam., narrowed above the sterile staminate flowers (ca. 1 cm above) to 6.5 mm diam., the remainder ca. 8.5 mm diam., obtuse at the apex. *Infructescences* (immature) 8 cm long, 2.6 cm diam., dark green on the outside, pale green within. Figs. 12, 17, 18.

DISTRIBUTION: *Syngonium meridense* is endemic to Venezuela and is known only from the state of Mérida.

Syngonium meridense is recognized by its simple leaf blades with short, rounded posterior lobes and basal veins free or nearly free to the base. It is most closely related to *S. chocoanum* from northern Colombia and western Panama. It differs from that species by its broader sinus and in having the tertiary veins distinct and wavy and in lacking any major branches from the primary lateral veins. *Syngonium chocoanum* has blades noticeably narrowed toward the base with a relatively narrow sinus. The latter species also has many conspicuous branches from the primary lateral veins (at least in the lower ⅓ of the blade), which form an acute angle with the primary lateral veins. The tertiary veins are obscure, close and markedly parallel, not distinct, remote and wavy as in *S. meridense*. It can also be confused in South America with *S. crassifolium* which differs in having larger leaves with longer, more angular lobes and basal veins which are united into a distinct rib (posterior rib).

A specimen with an immature inflorescence was collected in mid-December and a presumably full-sized fruit was collected in early April.

VENEZUELA: MÉRIDA: El Vigía/San Cristóbal del Táchira, *Bunting 2404B* (MY, VEN); Caño Zancudo-La Azulita, *Bunting 2800, 4381* (MY, VEN).

FIGURES 17–20.—17. *Syngonium meridense, Bunting 2404B*; juvenile leaves.—18. *S. meridense, Bunting 4381*; lower surface of adult plant showing wavy tertiary veins.—19. *S. sagittatum, Croat 48080*; preadult leaves ($\times 1/3$).—20. *S. sagittatum, Croat 48080*; adult leaves and unopened inflorescence ($\times 1/7$).

12. **Syngonium sagittatum** Bunting, Gentes Herb. 9:372. 1965. TYPE: Mexico, Oaxaca, Sierra de Juárez, at Vista Hermosa, 17.9 mi from bridge at Valle Nacional on road to Oaxaca, *Moore & Bunting 8920* (BH, holotype; MEXU, isotype).

Juvenile plants with stems ca. 1 cm diam., drying weakly verrucose with many slender longitudinal ridges; petioles broadly sheathed ca. ⅔ of their length; blades triangular-elliptic, 19–23 cm long, 7–9 cm wide, the anterior lobe acuminate at the apex, weakly constricted at the base, the posterior lobes narrowly triangular, rounded at the apex. Adult plants with stems to ca. 2 m long, short-creeping, closely appressed to trees; internodes green, 3–5.5 cm long, longer toward the base of the stem, 2.5–4 cm wide; petioles 37–43 cm long, sheathed ⅔ to ¾ its length, subterete, weakly flattened laterally above the sheath, the sheath open, thin along its margin; blades simple, subcoriaceous, ovate and conspicuously sagittate at the base, acuminate at the apex, 30–50 cm long, 23–31 cm wide, the upper surface semiglossy, light green, subbullate, the lower surface slightly paler, semiglossy, the margins revolute, the posterior lobes directed somewhat upward at an angle to midrib, usually unequal, rhomboid-triangular, obtusely angular at the apex, 12–18 cm long, usually longer than wide, frequently overlapping, the sinus spatulate to rhombic or obovate (clavate to hippocrepiform when pressed flat); primary lateral veins 9–11 pairs, prominently sunken; some interprimary veins prominently sunken; collective vein weakly sunken above, prominently to weakly raised beneath; basal veins 3–7 pairs, coalescing 1.5–7 cm from the petiole, the basal rib naked 1–5 cm. *Inflorescences* 2 or 3, erect; peduncles ca. 15 cm long; spathe thick and fleshy, 15–26 cm long; spathe tube ellipsoid, 8–11 cm long, 4.5–5 cm diam., greenish outside, tinged with violet purple inside, the constriction usually at a point about midway on the staminate portion of the spadix; spathe blade 14 cm long, long-acuminate and convolute at the apex (not fully flattened, even at anthesis), greenish white; pistillate portion of the spadix 2–4 cm long, 1.5–2.2 cm diam., slightly narrower at the apex, pale green, the synandrium irregularly 4–6-sided, smooth to bumpy at the apex, densely and minutely papillate, 6 mm long, 2–3 mm diam.; staminate portion of the spadix 10.5–13 cm long, 2–2.5 cm diam., broadest at about the middle. *Infructescences* green, pendent, weakly flattened, ca. 7 cm diam. in broadest view. Figs. 19, 20, 29.

DISTRIBUTION: *Syngonium sagittatum* is known for certain only from the Sierra de Juárez in eastern Oaxaca at elevations of 1200–1400 m. The area appears to be tropical wet forest.

The species is apparently most closely related to *S. crassifolium* of Colombia and Ecuador and has nearly identical leaves. It differs from that species in having a long-acuminate spathe. *Syngonium crassifolium* has a spathe which is acute or merely short-acuminate at the apex. Despite their similarities, it is doubtful that these two species are the same because of their very disjunct ranges and the fact that no other closely related plants have ever been collected between Mexico and Colombia-Ecuador.

Syngonium sagittatum is also related to *S. schottianum* and *S. hastiferum*, but of these two species it is most similar to the former, with which it shares a similar leaf shape and inflorescence. It differs from *S. schottianum* principally in

FIGURES 21–24.—21. *Syngonium llanoense*, *Croat 36946*; stem with young infructescences (×1/2).—22. *S. chiapense*, *Croat 48016*; adult blades with posterior lobes and infructescences (×1/4).—23. *S. crassifolium*, *Croat 38678*; adult blade (×1/3).—24. *S. crassifolium*, *Croat 38678*; juvenile infructescence (×½).

having a thinner blade which dries green rather than typically whitish as in *S. schottianum*.

The species is probably the same as *S. xanthosomaphyllum*, which was proposed as a new species by Birdsey (1955). However, the collection (*Birdsey 300*) from near Jalapa, Veracruz, has never been located. *Syngonium sagittatum* would certainly be expected to occur there and it is expected to be the same.

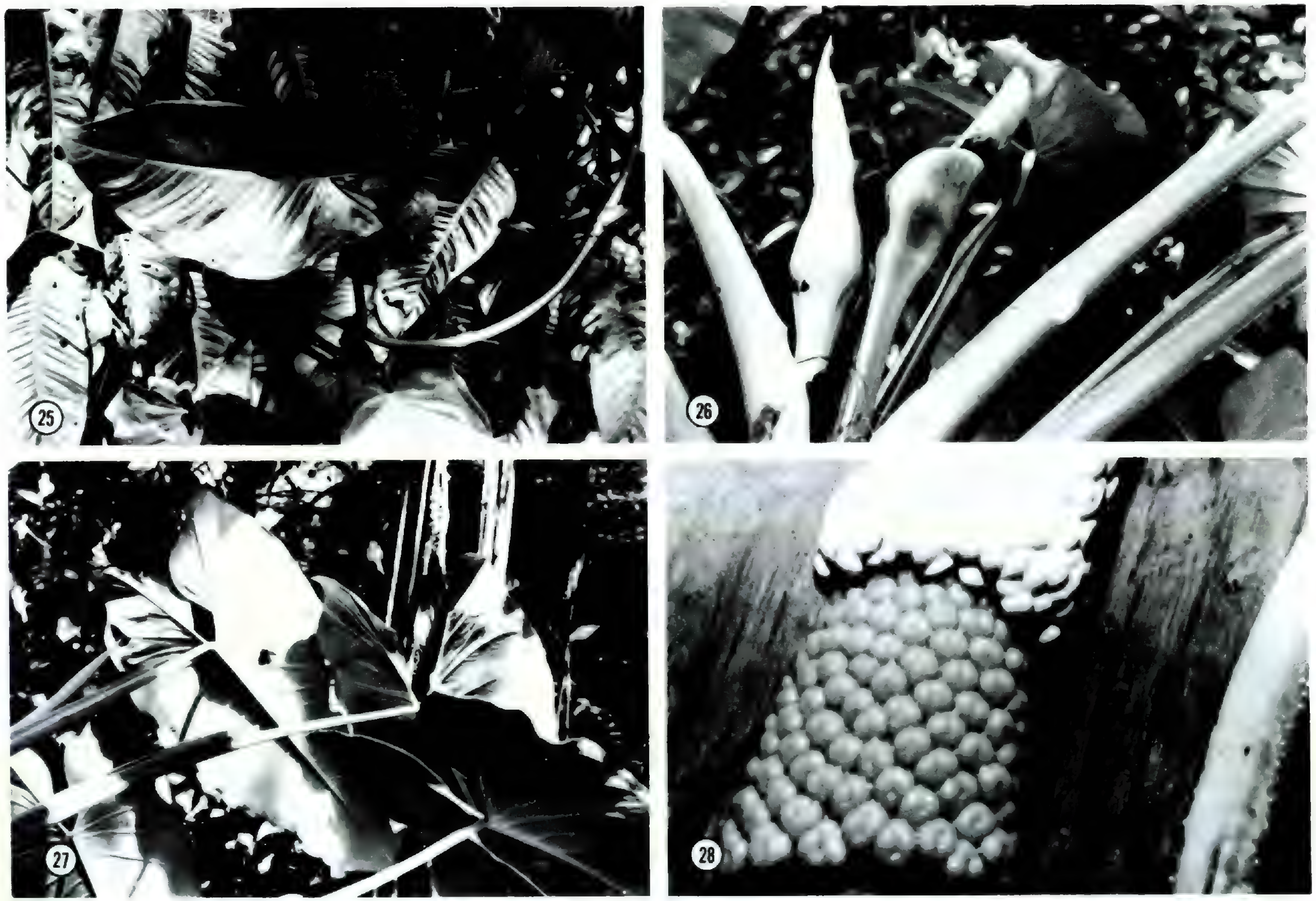
It has been collected in flower in February and September and in mature fruit in February.

MEXICO: OAXACA: Sierra de Juárez, *Bunting 1657* (BH, MEXU), *Croat 48004* (MO), *48080* (F, MEXU, MO, NY, SEL), *Moore & Bunting 8920* (BH, US).

13. **Syngonium schottianum** Wendl. ex Schott, Prodr. 200. 1860. TYPE: Costa Rica, *Wendland* (destroyed, type photo seen FM-12301).

Porphyrospatha schottiana (Wendl. ex Schott) Engler in A. DC., Monogr. Phan. 2:290. 1879.

Juvenile plants with scandent stems; internodes 10–20 cm or more, to ca. 1 cm diam., petioles sheathed beyond the middle, often to near the apex; blades ovate, becoming ovate-elliptic, with small lobes at base, the lobes rounded or angulate; venation conspicuous, the primary lateral veins sunken above, the tertiary veins clearly visible beneath. Adult plants epiphytic or hemiepiphytic creepers; stems to ca. 1 m long, ca. 4 cm wide; internodes very short; petioles 47–100 cm long, prominently sheathed except for the distal 5–13 cm, subterete above the sheath, weakly flattened near the blade attachment, the sheath firm, to 3 cm high near the base, tapering to 1 cm at the apex, with one margin shorter, the apex free, round, boat-shaped; blades lobed at the base, 40–60 cm long, 19–37 cm wide, dull on both surfaces, medium green above, much paler beneath, whitish, the posterior lobes directed slightly upwards and sometimes closing the sinus, sometimes slightly unequal, the sinus 6–14 cm deep, usually narrow, sometimes as broad as deep; basal portions of the major lateral veins sunken, the collective veins weakly visible, all other veins obscure on the upper surface; lower surface with the basal portions of the major lateral veins raised, arcuate-ascending and loop-connected with the major laterals, forming weak collecting veins, the innermost arising from the middle or lower ⅓ of the blade, the successive collective veins closely paralleling the first but becoming closer and more obscure toward the margin, spaced at intervals of 0.5–3 mm, each arising from the lower primary lateral veins and basal veins; basal veins 2–4, coalescing up to 1–4 cm from the petiole, the basal rib naked 1–6 cm. *Inflorescences* 4 per axil, each subtended by a prophyll ca. 25 cm long, 4 cm wide, conspicuously 2-ribbed on the outside surface, the ribs thin, ca. 4 mm high; peduncles 15–20 cm long, obtusely 3-sided; spathe tube green or green tinged with purple mostly in longitudinal streaks, pale violet purple inside, ca. 9–10 cm long at anthesis (to 17 cm long and 7.5 cm diam. in fruit); spathe blade whitish, ca. 10 cm long, constricted at its base and articulating along an elevated ring which forms 4–5 cm above the apex of the pistillate part of the spadix; spadix to 19.5 cm long; staminate portion of the spadix 19 cm long, 3 cm diam., white; pistillate portion of the spadix pale orange, 3.5 cm long on the open side, to 2.5 cm long on the back side, the stigmas bright yellow, irregularly rounded, 3.5 mm diam., ca. 1 mm high, with an irregular, often slitlike



FIGURES 25–28.—25. *Syngonium hastiferum, Croat 32919*; preadult leaf ($\times^1/_3$).—26. *S. schottianum, Croat & Folsom 33997*; petiole showing sheath, inflorescences (one unopened and one newly opened) ($\times^1/_4$).—27. *S. schottianum, Croat & Folsom 33997*; adult blades ($\times^1/_{10}$).—28. *S. schottianum, Croat & Folsom 33997*; inflorescence showing pistillate and sterile staminate flowers (above) ($\times$1.5).

depression in the center. *Infructescences* usually green, heavily tinged with purple, 14–16 cm long, 5–6 cm wide; fruiting spadix 7.5–10 cm long on the open side, 6–7 cm long on the back side, 3–5.5 cm diam., the surface pale brown; stigmas raised, ca. 2.8 mm wide, the central core ca. 1 cm diam.; seeds irregularly oblong, white, ca. 7 mm long. Figs. 26–28, 30.

DISTRIBUTION: *Syngonium schottianum* ranges from Honduras to Panama but is also likely to range into Colombia. The species has been collected in Costa Rica only on the Atlantic slope in Alajuela and Heredia. It is restricted to the Atlantic slope except at middle elevations along the Continental Divide in central Panama. It ranges from near sea level to about 900 m in wetter parts of tropical moist forest, premontane wet forest, and tropical wet forest.

See the discussion of *S. sagittatum* for possible relationships with that species. The species is closest to *S. crassifolium* from Colombia and Ecuador, but it differs from that species by its pale lower blade surface and its generally larger inflorescences.

Flowering inflorescences have been found from February through August. Nearly mature fruits are known from July.

COSTA RICA: ALAJUELA: NE of Quesada, *Croat 46950* (MO); Near Upala, *Croat 36261, 36445* (MO). CARTAGO: NE of Turrialba, *Croat 43367* (MO). HEREDIA: Near Puerto Viejo, *Croat 35686, 35759* (MO). LIMÓN: S of Punta Cahuita, *Croat 43190, 43196* (MO).

HONDURAS: OLANCHO: N of Catacamas, *Standley 18745* (F).

NICARAGUA: RÍO SAN JUAN: NE of El Castillo, *Neill & Vincelli 3617* (MO). ZELAYA: Vicinity of Matagalpa, *Stevens 7516* (MO).

PANAMA: BOCAS DEL TORO: W of Almirante, *Croat 38210* (MO); Station Milla 7.5, *Croat 38114* (MO). CHIRIQUÍ: Vicinity of Fortuna Dam site, *Croat 48710* (MO). COCLÉ: Vicinity of El Copé, *Hammel 2632* (MO), *Croat 49148* (MO); La Mesa, *Croat 13421, 37406* (MO); Cerro Pilón, *Lallathin 5004* (MO), *Croat 14363* (MO); N of Cerro Pilón, *Croat 37568* (MO), COLÓN: Vicinity Guásimo, *Croat 9959* (MO), *9935* (MO, SCZ); Near Portobelo, *Kennedy 480* (F), *Croat 36972* (MO). PANAMÁ: NE of Alto de Pacora, *Croat 22730* (MO); Cerro Campana, *Croat 17244, 25223, 35984* (MO). VERAGUAS: Escuela Agrícola Alto Piedra, *Croat 25542, 27339, 48974* (MO), *Croat & Folsom 33997* (MO); Near Santa Fe, *Croat 33991A* (MO).

C. **Syngonium** section **Pinnatilobum** Croat, sect. nov. TYPE SPECIES: *Syngonium steyermarkii* Croat.

Lamina adulta profunde lobata incisa; petiolus vaginatus ad medium usque; lamina juvenalis simplex, ovata, basi cordata; lamina intermedia incisa magis.

14. **Syngonium steyermarkii** Croat, sp. nov. TYPE: Guatemala, San Marcos, vicinity of San Rafael, Finca Armenia at La Trinidad, ca. 2 km above main buildings of finca, 1100–1250 m, virgin forest along stream, *Croat 40842* (MO-2599645, holotype; EAP, F, MEXU, PMA, US, USCG, VEN, isotypes).

Caudex haud glaucus, scandens, internodiis 2–4 cm longis, 1–3 cm latis; foliorum petiolus 25–60 cm longus, ca. ad ½ longitudinalis usque vaginatus; lamina incisus lobo, ambito ovata, 20–43 cm longa, 17–36 cm lata, lobus anticus segmentis 5–6, 2–5 cm latis. Inflorescentia in axilla 1–7, pedunculus 7–13 cm longus; spathae tubus 2.6 cm longus, 2 cm latus; pedunculus et spathae tubus valde glaucus.

Hemiepiphytic creeper; sap milky; stems 1–3 cm diam., 1.3 m long; upper internodes 1.5–2.5 cm long, dark green, shiny, drying light brown, shiny, the periderm drying wrinkled; leaves ca. 8, persisting only near the apex, broadly spreading; petioles 25–60 cm long, subterete, sheathed to beyond the middle to upper ⅔, sharply ribbed near the apex of the sheath, drying black; blades incised-

lobate, ovate in outline, 20–43 cm long, 17–36 cm wide, firmly membranous, medium green above, paler beneath, drying black, the anterior lobe with 5 or 6 segments, shallowly lobed to within 1–2 cm distant from the midrib, the segments 2–5 cm wide, narrowly rounded at the apex, the posterior lobes about half as long as the anterior lobe, the segments partly confluent; midrib and primary lateral veins sunken above, raised and U-shaped beneath; secondary veins and collective vein weakly sunken on the upper surface, weakly raised on the lower surface; tertiary veins distinctly visible. *Inflorescences* 1–7 per axil; peduncles terete, erect in flower, 7–13 cm long, ca. 1 cm diam., straight to sigmoid; spathes 5.5–7 cm long, somewhat fleshy, narrowly ovoid, acuminate, tightly inrolled and curved forward at the apex, scarcely constricted near the middle, opening from the apex of the spadix to the base of the spadix; spathe tube green, glaucous, grayish or whitish green, ca. 2.6 cm long, 2 cm diam.; spathe blade green, scarcely or not at all flared open; spadix 5–5.5 cm long; pistillate portion of the spadix 2.6–3 cm long, 2 cm diam., broader than the staminate portion, the pistillate flowers pale green, 4–5 mm diam., the stigma sessile, ca. 2 mm diam., orange yellow; staminate portion of the spadix 2–2.5 cm long, 0.6–1.3 cm diam., the staminate flowers creamy white, the synandrium truncate at the apex with a medial depression, irregularly 4–6 sided, 2–3 mm diam. *Infructescences* with the spathe tube 6–7 cm long, 3.5–4 cm diam., in part weakly glaucous, obtusely ribbed on the closed side; fruiting spadix 5–7 cm long, ca. 4 cm diam. Figs. 31, 37–39.

DISTRIBUTION: *Syngonium steyermarkii* is known only from the Pacific slope of Guatemala and southeastern Mexico at elevations above 1250 m.

The species is named in honor of Julian A. Steyermark who made three collections of it between 1940 and 1942 in three different departments of Guatemala.

Syngonium steyermarkii is unique in having incised-lobate leaves like those of *Philodendron radiatum* Schott. It also differs from other *Syngonium* species in having the inflorescences all mature at about the same time and having the pistillate part of the spadix appreciably larger than the staminate portion.

The data on the flowers was provided by Josef Bogner from a living collection of *Croat 47201* growing at Munich.

The type collection had immature fruits in July.

GUATEMALA: QUEZALTENANGO: Between Finca Pirineos and Patzulín, *Standley 86886, 86900* (F); Along Quebrada Geronimo, Finca Pirineos, S slope of Volcán Santa María, 1300–2000 m, *Steyermark 53437* (F). SAN MARCOS: Finca El Porvenir along Río Chopal, S slope of Volcán Tajumulco, 1300–1500 m, *Steyermark 37499* (F); Above San Raphael, *Croat 40842* (MO). SUCHITEPIQUEZ: Volcán Santa Clara between Finca El Naranjo and upper slopes, 1250–2650 m, *Steyermark 46621* (F).

MEXICO: CHIAPAS: N of Puente Monte Perla, *Croat 47201* (MICH, MO).

D. Syngonium section **Syngonium** Croat, sect. nov. TYPE SPECIES: *Syngonium auritum* (L.) Schott.

Lamina adulta trisecta aut 5–11-pedatisecta; segmenta lateralia valde inaequilateralia; petiolus e $^1/_3$ ad $^4/_5$ longitudinis usque vaginatus; lamina juvenalis ovata aut elliptica; lamina intermedia sagittata aut hastata.

15. Syngonium angustatum Schott, Oesterr. Bot. Z. 8:175. 1858. TYPE: Nicaragua, Chontales, Punta Poderoso, *Oersted* (C).

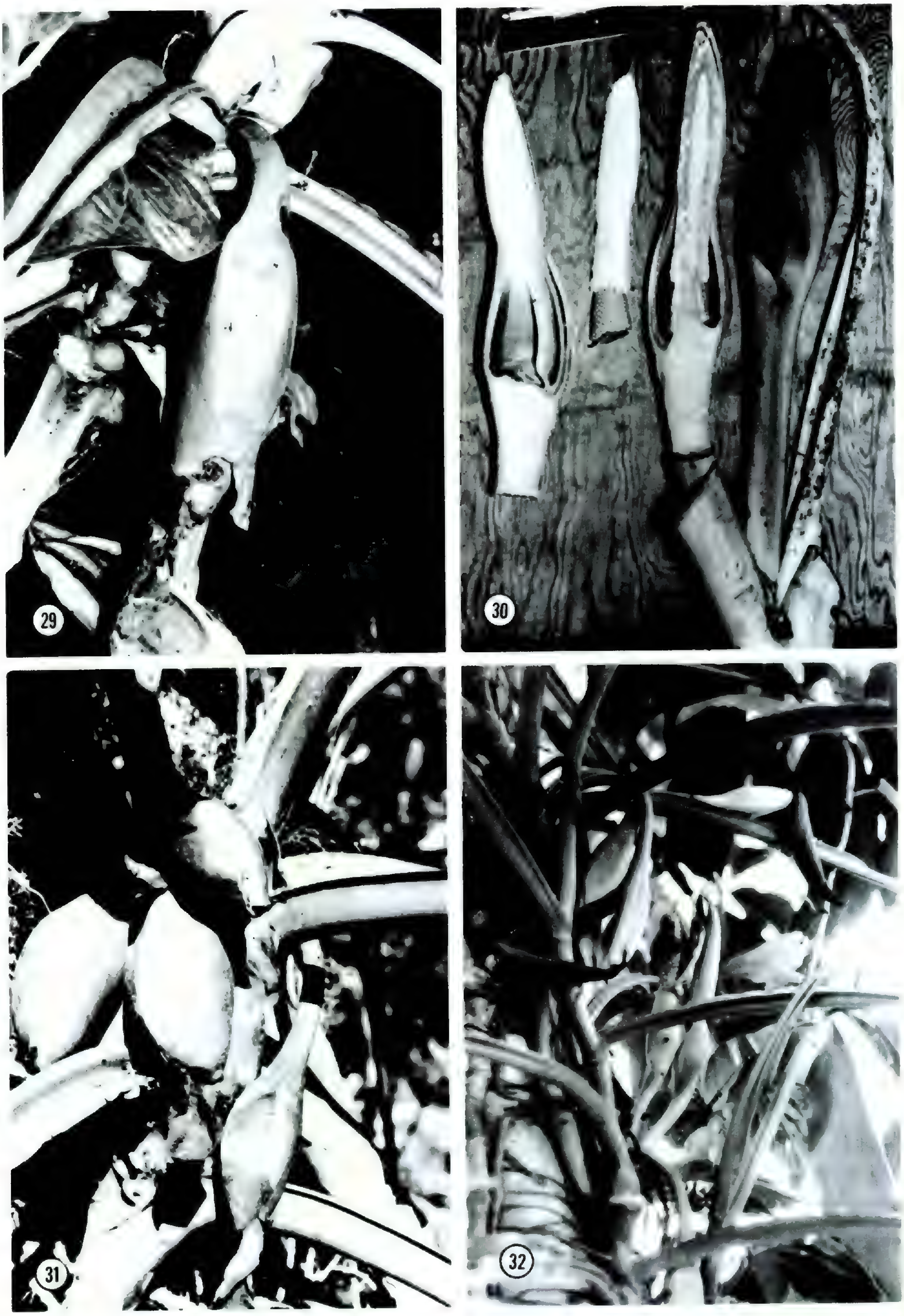
S. oerstedianum Schott, Oesterr. Bot. Z. 8:178. 1858. TYPE: Costa Rica, Guanacaste, *Oersted* (c, not seen); Schott drawing 3214 (NYBG photo 4332).
S. albolineatum hort., H. G., Bull's Catalogue p. 6. 1871. LECTOTYPE: *N. E. Brown*, Feb. 27, 1877. (Specimen from the type plant of Hort. Bull) (K).
S. podophyllum Schott var. *albolineatum* (Hort.) Engler, Pflanzenr. IV.23E (Heft 71):129. 1920.
S. podophyllum var. *oerstedianum* (Schott) Engler, Pflanzenr. IV.23E (Heft 71):129. 1920.
Nepthytis triphylla hort. Nash ex L. H. Bailey, in Cycl. Amer. Hort. 3:1076. 1901. TYPE: (not seen, fide Birdsey, 1955).
Syngonium gracilis Matuda, Anales Inst. Biol. Univ. Nac. Mexico 43, Ser. Bot. 1:56–57. 1972, non (Miq.) Schott. TYPE: Mexico, Oaxaca, Palomares, Juchitán, near Río Coatzacoalcos, 200 m, *MacDougall 804-4* (MEXU, holotype).

Juvenile plants with stems not glaucous, usually sparsely muricate; petioles sheathed usually less than ⅓ their length; blades dark green, marked on the upper surface along the principal veins with gray green, cordate, less than 6 cm long, the anterior lobe ovate, the posterior lobes suborbicular; intermediate leaves sagittate or hastate, acuminate at the apex. Adult stems not glaucous, sparsely muricate; internodes mostly 2–10 cm long on the flowering stems; petioles sometimes pruinose, sheathed ½–⅘ their length, 15–40 cm long; blades pedatisect, dark green above, sometimes grayish green on the midrib and rarely on the lateral veins; leaflets 3–11, usually conspicuously free from one another, the lowermost auriculate, the median leaflet elliptic to oblong-elliptic to oblanceolate, acuminate at the apex, attenuate, acute or cuneate at the base, 11–31 cm long, 4–10 cm wide, the rachis gradually curved, the lateral leaflets inequilateral, the inner margin acute to cuneate, the outer margin rounded to auriculate, the auricle rounded to bluntly acute, rarely slightly pinched off; primary lateral veins 3–5 pairs, sunken above, raised beneath; tertiary veins distinct. *Inflorescences* to ca. 7 per axil; peduncles glaucous, almost 3-sided, 5–10 cm long, and erect at anthesis, to 17 cm long and pendent in fruit; spathe 7 to 14 cm long; spathe tube elliptic, 2–5 cm long, 1.0–2.5 cm diam., green and usually glaucous outside, green inside; spathe blade cream on both surfaces, 6–9 cm long, 1.5–3.5 cm wide, acuminate at the apex; pistillate portion of the spadix 1.3–2.6 cm long, 5–10 mm diam., greenish, the flowers irregularly hexagonal, the stigma discoid; staminate portion 2.5–6.5 cm long, 5–15 mm diam., pale yellow, the flowers completely fused into a synandrium with no sign of fusion, the apex conspicuously retuse. *Infructescences* usually bright red, sometimes reddish orange, sometimes glaucous; fruiting spadix brown, 2.5–4.5 cm long, 1.5–2.5 cm diam. Figs. 32, 40, 45.

DISTRIBUTION: *Syngonium angustatum* ranges from Mexico (southern Tamaulipas) through Belize, Guatemala, Honduras and Nicaragua to northern Costa Rica. It is cultivated in Panama. Although most abundant at lower elevations, it ranges up to 700 m (to 1000 m, fide Birdsey, 1955). The species is most abundant in tropical moist forest life zones, but has been collected in tropical dry forest in Nicaragua and Costa Rica.

Syngonium angustatum is closest to *S. podophyllum* but can usually be distinguished by its more uniformly slender leaflets, the papillae of the older stems, and the deeply retuse, fused staminate flowers (also see the key). According to Birdsey (1955) the species hybridizes with *S. podophyllum* in Mexico.

Syngonium angustatum apparently flowers most abundantly during the early rainy season with some flowering during the dry season as well.



FIGURES 29–32.—29. *Syngonium sagittatum, Croat 48080*; stem and infructescence $(\times {}^{1}/_{4})$.—30. *S. schottianum, Croat & Folsom 33997*; longitudinal section of inflorescence showing half of spathe (left) and half of spadix (right) removed $(\times {}^{1}/_{4})$.—31. *S. steyermarkii, Croat 40842*; stem and infructescences $(\times {}^{5}/_{12})$.—32. *S. angustatum, Croat 41699*; stem, inflorescences (erect, young infructescences pendent) $(\times {}^{1}/_{4})$.

BAHAMAS: Eleuthera, *Correll 49000* (NY).

BELIZE: Maskall Pine Ridge, *Gentle 1144* (F, G, MICH, NY). BELIZE: Northern Highway, *Dwyer & Liesner 12043* (GH, MO, NY); SW of Belize, *O'Neill 8257, 8542* (MICH). CAYO: S of Grano de Oro, *Croat 23403* (F, MO), *23781* (MO), *Dwyer 10890* (MO); Roaring Creek, *Wiley 246* (MO); Near Augustine, *Spellman 1584* (MO). COROZAL: Between Corozal and Pachacen, *Gentile 62* (F), *Lundell 4935* (F, NY); No other location, *Gentle 459, 616, 502* (MICH). STANN CREEK: W of Stann Creek, *Croat 24205* (MO). TOLEDO: N of Columbia Forest Station, *Croat 24232* (MO); Punta Gorda, *Croat 24469* (F, MO); Temash River, *Dwyer 12885*, (MO).

COLOMBIA: Island of Providencia, *Proctor 3476* (US).

COSTA RICA: ALAJUELA: Vicinity of Los Chiles, *Holm & Iltis 812* (A). GUANACASTE: S of Peñas Blancas, *Liesner 4658* (MO).

GUATEMALA: ALTA VERAPAZ: Eastern portions, *Watson & Sereno 104* (GH); E of Panzos, *Croat 41699* (MO). IZABAL: SW of Puerto Barrios, *Croat 41836* (MO), *Standley 72127, 72565* (F). PETÉN: Uaxactún, *Bartlett 12664* (MICH, US); La Libertad, *Lundell 2432* (MEXU, MICH), *2544* (GH), *3213* (F); National Park of Tikal, *Ortiz 333* (F). ZACAPA: N from Route CA9, *Croat 41882* (MO).

HONDURAS: COLÓN: W of Trujillo, *Murry 449* (MO); Vicinity of Cuidad de Castilla, *Nelson & Martínez 1191* (TEFH). CORTES: SW of Omoa, *Croat 42559* (MO); Road to Chamelecón Cafradia, *Molina 3849* (GH, F); SW of Puerto Cortés, *Nelson et al. 3020* (TEFH). GRACIAS A DIOS: Mosquitia, *Clewell & Cruz 4050* (GH, MO); Puerto Lempira, *Nelson 4846* (TEFH). OLANCHO: Dulce Nombre de Culmí, *Nelson & Clewell 438* (MO, TEFH).

MEXICO: No other location, *Sandoval 6* (US). CAMPECHE: Tuxpeña, *Lundell 815* (F, MICH, US). CHIAPAS: Vicinity of Palenque, *Croat 40137, 40315* (MO), *Matuda 3825* (GH, MICH, MEXU). OAXACA: N of Matias Romero, *R. M. King 841* (MICH, US); Palomares, *MacDougall 804A* (MEXU); Tuxtepec, *Sousa 1859* (MEXU). PUEBLA: Forest of Ajeujihe, *D. R. Canta 520* (MEXU). SAN LUIS POTOSÍ: Tamazunchale, *M. T. Edwards 581* (MO). TABASCO: Villahermosa, *Bunting 1652* (BH, MO), *Spellman et al. 115* (MO). VERACRUZ: San Andrés Tuxtla, *Dressler & Jones 16* (GH); Vicinity Juan Rodríguez Clara, *Gómez-Pompa & Valdés 1727* (MO); Vicinity Sayula San Juan Evangelista, *Leija & Garza 8137* (MEXU); Tampico, *Nevling & Gómez-Pompa 426* (MEXU); Vicinity Camp Hnos, *Valdiva 1184* (JALAPA, MEXU). YUCATÁN: Chichen Itza, *Steer 1629* (MICH); Izamal, *Greenman 452* (F).

NETHERLANDS ANTILLES: Bonaire, *Arnoldo 2296* (US).

NICARAGUA: BOACA: N of Río Las Cañas, *Stevens 5848* (MO); Vicinity Río Quilan Bridge, *Stevens 9323* (MO). CARAZO: Near Jinotepe, *Standley 8576* (F). CHONTALES: La Libertad, *Standley 8904* (F), *Stevens 4091, 4092, 4204* (MO); Road to Cuapa, *Stevens 3654, 6470* (MO). GRANADA: Volcán Mobacho, *Atwood & Neill AN90* (MO). MANAGUA: Vicinity of National School of Agriculture, *Seymour & Atwood 2228* (MO); Tipitapa, *Atwood & Seymour 3424* (GH, NY, UC), *Croat 39051* (MO), *Garnier 774* (US), *Neill 7260* (MO), *Stevens 9509* (MO). MATAGALPA: Summit of El Toma Road, *Neill 1572* (MO); Between La Danta and La Luna, *Stevens 9573* (MO). NUEVA SEGOVIA: N of Jalapa, *Neill 1608* (MO). RIVAS: Isla de Ometepe, *Stevens 6640* (MO). ZELAYA: Near Bluefields, *Hamblett 613* (MO); SE of Cerro San Isidro, *Proctor, Jones & Facey 27048* (NY); Along Caño Majagua, *Stevens 6983* (MO); Vicinity of San José del Hormiguero, *Stevens 7006, 7047* (MO); Near Tala Has and Puente Mango, *Stevens 7639* (MO); SW of Río Wawa, *Stevens 7924* (MO).

PANAMA: CANAL ZONE: Stevens Circle, Balboa, *Croat 9181* (MO); Summit Gardens, *Croat 17059* (MO).

THAILAND: BANGKOK: Cultivated at Kasetsart University Nursery, *Nicolson 1691* (B).

16. Syngonium atrovirens Bunting, Acta Bot. Venez. 11:323. 1975. TYPE: Venezuela, Zulia, Hacienda Raizado (Hda. San Benito), ca. 1 km S of Concha, *Bunting 2776* (MY-0254, holotype; VEN, isotype).

S. apurense Bunting, Acta Bot. Venez. 11: 322. 1975. TYPE: Venezuela, Apure, Reserva Forestal San Camilo, 7 km E of La Ceiba, 16 km E of El Jordan, 200 m, *Steyermark, Bunting & Blanco 101942* (MY, VEN).

Scandent hemiepiphytes. Juvenile plants with petioles sharply sulcate, the margins narrowly winged; blades dark green, glossy above, pale beneath. Adult plants with stems 1.3–1.5 cm diam., gray glaucous when young, the epidermis brown and cracked in age; lower internodes 6–9 cm long, the upper internodes 2–4 cm long; petioles 25–35 cm long, gray glaucous, sheathed except for the upper 5–9 cm, the sheath inrolled, sometimes with elevated whitish striations,

the unsheathed part sharply angular-winged adaxially, the lateral margins sharp, narrowly winged; blades trisect, thin to subcoriaceous, 20–25 cm long, dark green and often glaucescent above, paler green beneath, semiglossy; leaflets usually markedly free and petiolulate rarely confluent, the petiolules 5–15 cm long, rarely sessile; median leaflet elliptic to elliptic-ovate or oblong-elliptic, acuminate at the apex, obtuse to acute and attenuate at the base, 17–30 cm long, 5–11 cm wide, the primary lateral veins 4–5(–9) per side, weakly sunken, arising at an angle of (65–)70–80°(–90°), weakly curved to the collective vein, the tertiary veins distinct, the primary collective vein 2–6 mm from the margin, generally more or less straight, the margins sometimes finely undulate; lateral leaflets acute to narrowly rounded at the apex, slightly shorter than the median leaflet, the inner margin cuneate-acute, the outer margin prominently auriculate, the auricles acute to narrowly rounded at the apex, rarely broadly rounded with the auricles overlapping on the blade whose leaflets are not fully free, the primary lateral veins arising at a generally sharper angle than those of the median leaflets (ca. 50–60°). *Inflorescences* solitary; peduncles gray glaucous, 5–7 cm long, 6–9 mm diam. at anthesis, soon recurved; spathe 11–15.5 cm long; spathe tube narrowly oblong-ovoid, 5.5–7.2 cm long, 1.5–3.5 cm diam., not markedly constricted below the blade, semiglossy, light green on the outside, paler green within; spathe blade boat shaped when open, obtuse at the apex, cream colored on the outside, creamy white within, weakly tinged with pink toward the base; spadix sessile, 11 cm long, ca. 3 cm shorter than the spathe; pistillate portion of the spadix 1.6 cm long, 1.5 cm diam. (7 mm on drying); staminate portion of the spadix 8.5 cm long (dried), the sterile staminate portion 1.2–2.5 cm long, constricted weakly beneath the fertile part of the spadix. *Infructescences* pendent, 8–9 cm long, 2.5 cm diam. (dried); syncarp ovoid-elliptic, only slightly shorter than the fruiting spathe. Figs. 33, 34.

DISTRIBUTION: *Syngonium atrovirens* is known for certain only from Venezuela and has been collected at elevations of 50–500 m in the states of Apure, Táchira, Mérida, and Zulia. A sterile collection by André (*419*) from the Magdalena River Valley of Colombia (Naranjo-Carare) is probably also this species.

The species is closely related to *S. yurimaguense* from the upper Amazonian forests of Peru and Bolivia but differs from that species by its inflorescence which is much less constricted above the spathe tube. Both species have in common very similar leaves which have the primary lateral veins of the median leaflet arising from the midrib at almost a 90° angle.

VENEZUELA: APURE: East of Ceiba, *Steyermark et al. 101942* (MY, VEN); SE of Caserio San Camilo, *Steyermark et al. 101478* (VEN). MÉRIDA: SE of El Vigía and El Quince, *Bunting 2404A* (MO, MY, VEN). TÁCHIRA: La Fria-La Grita at Las Pavas, *Bunting 2494* (MY, VEN). ZULIA: S of Concha, *Bunting 2776* (MY, VEN); Sierra de Perijá, *Steyermark & Fernández 99633* (NY, US, VEN).

17. Syngonium auritum (L.) Schott, Wiener Z. Kunst 3:780. 1829.

Arum auritum L., Sp. Pl. ed. 2, 1371. 1763. TYPE: Species No. 1079-17 in Linnaean Herbarium (LINN).
Caladium auritum Vent. ex Willd., Spec. Pl., ed. 4, 4 (Part 1):491. 1805. TYPE: Jamaica? (not seen).
Syngonium plumieri Schott, Prodr. Syst. Aroid. 206. 1860. TYPE: Santo Domingo, *Plumier* (not seen).

Juvenile plants with stems scandent; blades ovate, acute at the apex, sagittate to hastate at the base. Adult stems hemiepiphytic, somewhat scandent, slightly

glaucous, 1.5–2 cm diam.; internodes 4–9 cm long, with one large feeding root and several clasping roots per node (fide Birdsey, 1955); petioles 15–48 cm long, broadly sheathed usually 4/5 their length (rarely to 2/3); blades usually trisect or sub-5-pedatisect, rarely 5 pedatisect, the lobes confluent, the median lobe 10–30 cm long, 6–20 cm wide, broadly elliptic, abruptly acuminate at the apex, the base obtuse, the tissue continuous with the lateral lobes, the first pair of lateral lobes ovate to elliptic, 6–21 cm long, 3–11 cm wide, acute at the apex, strongly inequilateral, usually conspicuously auriculate on the outer side at the base, the auricle sometimes free, then 4–10 cm long, to ca. 4 cm wide, the upper surface semiglossy, medium green, the lower surface paler; primary lateral veins mostly 5–7 pairs, joining the midrib at a 20–45° angle. *Inflorescences* to 3 per axil; peduncle 7–13 cm long; spathe tube cylindroid, 4.2–8.5 cm long, 1–1.9 cm diam., dark green outside, green inside with a suffusion of bronzy red at the base; spathe blade ovate in outline when opened, mucronate at the apex, conspicuously constricted at the base, 12–18 cm long, 7–10 cm wide (flattened), creamy white on both sides, sometimes greenish white on the outside and creamy white tinged faintly with violet purple within; spadix extending to ½ as high as the spathe blade; pistillate portion of the spadix 3.4–4.8 cm long, 9–12 mm diam., the flowers mostly rhombic to 5- or 6-sided, the stigma discoid, dark yellowish green (fide Birdsey, 1955); staminate portion of the spadix 3.5–9.2 cm long, rounded at the apex, slightly attenuate toward the apex, the sterile staminate section 7–17 mm long, creamy white, oblong, slightly attenuate at the apex, the sterile staminate flowers larger and more irregular than the fertile staminate flowers, the fertile staminate flowers 2–5 (usually 4), the synandrium retuse at the apex, the stamens fused together only on the inner side. *Infructescences* pendent; fruiting spadix 7–7.8 cm long, 1.4–2 cm diam. Figs. 35, 36.

DISTRIBUTION: The species is known from Jamaica, Cuba and Hispaniola in the West Indies. It is the type species for the genus. The species can be recognized by its elongate spathe tube and the spathe blade which is up to twice as long as the staminate part of the spadix. An unnumbered Hitchcock collection at MO from Lucea, Jamaica, is anomalous in having the median lobe with a conspicuously sinuate margin. The species frequently has weakly irregular margins and the Hitchcock collection seems to be merely a gross exaggeration of this character.

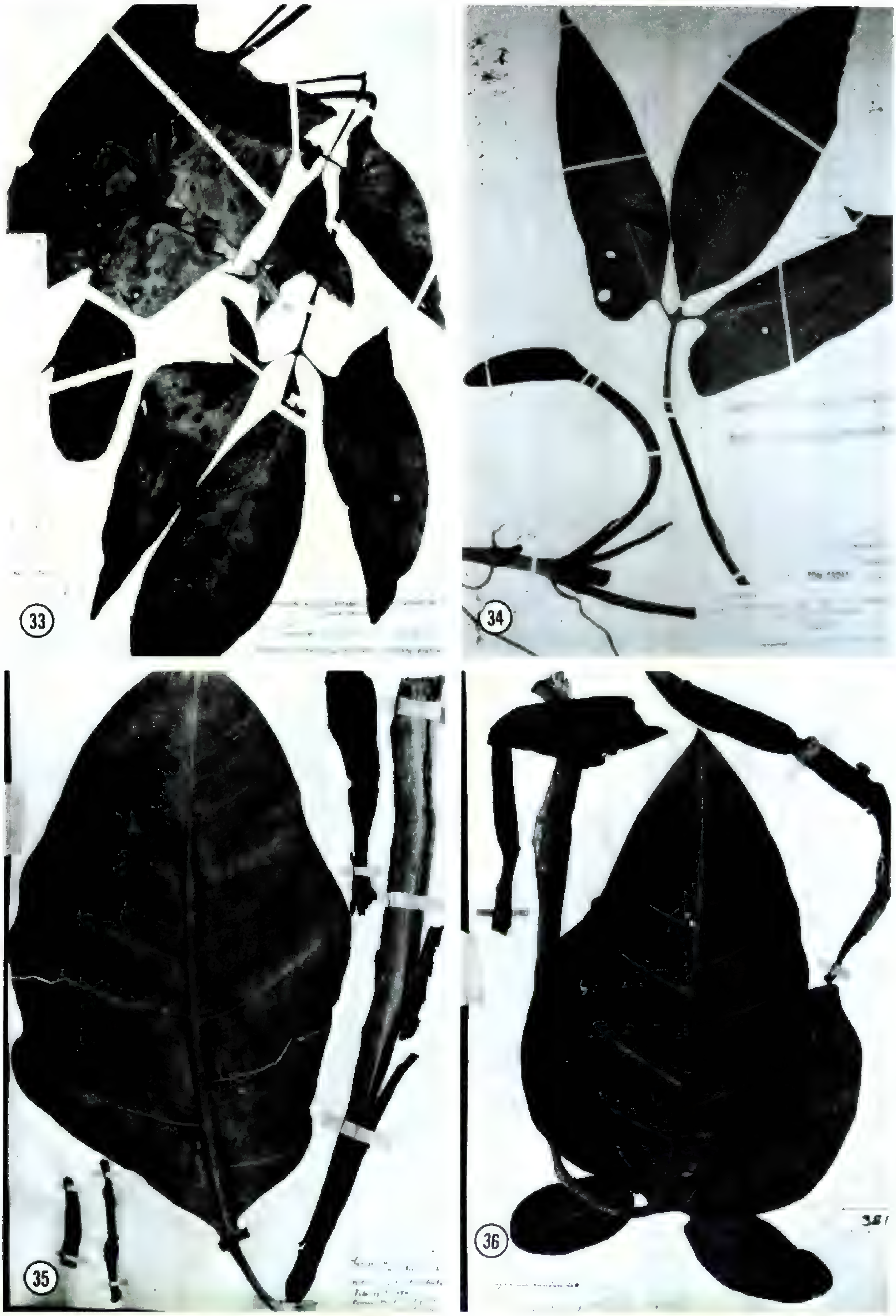
According to Birdsey (1955) the species may flower all year but no particular individual is in flower continuously.

CUBA: Principes, near railroad, *Shafer 421* (CM).

HAITI: DUNORD: Trail between Milot and Citadel, *Fairchild s.n.* (US); Port Margot to Cornell, *Nash 185* (NY); Vicinity of Dondon, *Leonard 8671* (US). NORDOUEST: Vicinity of Bassin Bleu, *Leonard 14894* (US). Ile de la Gonave, vicinity Anse Galette, *Leonard 3078* (US).

JAMAICA: HANOVER: Lucea, *Hitchcock s.n.* (MO). MANCHESTER: Bethany, *Wolle s.n.* (CM); Mande Ville, *Britton 1053* (NY). PORTLAND: Port Antonio, *Hitchcock s.n.* (MO); Stony River Base Camp, 1250 ft, *Morley & Whitefoord 686, 708* (MO). ST. ANDREW: Kingston, Hope Gardens, *Skutch s.n.* (F). ST. CATHERINE: Bog Walk, *Hitchcock s.n.* (MO). ST. THOMAS: Fountain Inn, 500 ft, *Yuncker 17526* (F, MICH); House Hill, *Maxon 9047* (NY, US). TRELANY: Windson, *Miller 1455* (US).

18. Syngonium erythrophyllum Birdsey ex Bunting, Baileya 14:17. 1966. TYPE: Panama, Canal Zone, near Fort Randolph near the Atlantic coast, *Maxon & Harvey 6536* (US, holotype).



FIGURES 33–36.—33. *Syngonium atrovirens, Steyermark & Fernandez 99663*; adult plant with mature infructescence.—34. *S. atrovirens, Bunting 2776*; adult plant with juvenile infructescence. 35. *S. auritum, Lynch s.n.*; median segment of adult blade with petiole and loose spadix (×1/3).—36. *S. auritum, March 1433*; adult blade with inflorescence.

Juvenile plants often solitary; stems with short internodes, later scandent, branching, slender, leafy; blades ovate, 3–9 cm long, ± cordate at the base, the lobes rounded, the sinus ± arcuate with the decurrent petiole, the upper surface blackish green, the lower surface at first green, soon becoming deep violet purple; juvenile blades on climbing stems larger, simple, sagittate, dark green above, deep violet purple below, 9–17 cm long, becoming indistinctly 3-lobed; petioles 11–20 cm long, sheathed to near the apex. Adult plants with stems sometimes branching, green, not glaucous, usually less than 1 cm wide, the periderm thin, minutely papillate, flaking and pale reddish brown at maturity; petioles 9–20 cm long, sheathed $^{4}/_{5}$ or nearly throughout its length; blades trisect, subcoriaceous, the surface dark green and shiny above, paler beneath, usually green, sometimes violet purple; leaflets usually completely free, spreading or slightly overlapping, acuminate to rounded at the apex, ending abruptly with a minute apiculum; median leaflet elliptic to lanceolate-elliptic or narrowly ovate, 10–22 cm long, 4.5–10 cm wide, obtuse to attenuate at the base; lateral leaflets 4.5–10 cm long, 1.2–4.3 cm wide, elliptic to lanceolate or oblong, obtusely and narrowly rounded at the apex, the base inequilateral but not auricled. *Inflorescences* usually 2 or 3 per axil; peduncles 3–11 cm long, green, not glaucous, erect at anthesis, pendent in fruit; spathe equalling or longer than the spadix; spathe tube green, 2–4 cm long, 1–1.5 cm diam., ovoid to ellipsoid; spathe blade white, ovoid to ellipsoid (when flattened), 8–11 cm long, 5–6 cm wide, weakly reflexed away from the spadix at anthesis; spadix 9–13.5 cm long; pistillate portion of the spadix to 1.5–1.8 cm long, the pistils ca. 1.4 mm diam., the stigmas discoid, ca. 0.9 mm diam.; staminate portion of the inflorescence 6.5–10 cm long, (the fertile part 6–9 cm long), the flowers 4-androus, truncate or slightly retuse at the apex, the pollen white in arachnoid clusters. *Infructescences* ovoid, yellowish green, 3–5 cm long, the tube opening at maturity; seeds white, ± oblong, rounded on one end, apiculate and angled on the other end, 6–7 mm long. Figs. 41, 46.

Distribution: *Syngonium erythrophyllum* is known only from Panama at elevations from sea level to 350 m in tropical moist forest and premontane wet forest life zones. Birdsey (1955) reports that this species may also occur in the Reventazón Valley of Costa Rica (provinces of Cartago and Limón) because he saw similar juvenile leaves on *Syngonium* plants collected there.

It is not confused with any other species and is recognized by its thick, trisect, slightly auriculate leaves with violet purple lower surfaces, at least on juvenile blades. Stems dry with a conspicuous, flaky, reddish brown periderm. The frequently rounded and apiculate-tipped leaflet apices are another useful character in recognizing the species.

On Barro Colorado Island this species produces abundant juvenile plants but few adult plants were seen during more than three years of field work there.

Flowers have been found mostly March–June and fruits in August–September.

Panama: canal zone: Barro Colorado Island, *Birdsey 349* (UC, US), *Croat 6208, 8637, 9124, 11709* (MO), *11778* (F, MO, US), *14955* (F, MO), *Knight s.n.* (US); Near Fort Randolph, *Maxon & Harvey 6536* (US), *Shattuck 31* (F), *Wetmore & Woodworth 31, 875* (F, GH). panamá: El Llano-Cartí Road, *Croat 33800, 34801* (MO), *Folson 2258* (MO).

19. Syngonium gentryanum Croat, sp. nov. type: Peru, Huánuco, La Divisora, Tingo María-Pucallpa, road near Loreto border, 1150–1250 m, premontane

rain forest, *Gentry, Daly & Cruz 18822* (MO-2415210, holotype; USM, isotype).

Caudex ca. 2 cm diam.; lamina trisecta; petiolus ad 63 cm longus; vagina 16–28 cm longa, lamina media oblonga-elliptica, 27 cm longa, 9.3 cm lata; lobi laterales lobum medium aequantes, inaequalateres haud auriculatos. Inflorescentia 2 in axilla; pedunculus 7 cm longus; spathae tubus oblongus-ellipticus, 2.5–3.5 cm longus, 1.1–2.3 cm diam.; spathae lamina elliptica, acuminata; spadix ca. 8 cm longa, parte feminea spadicis 7 mm longa, 4 mm diam.

Adult plants with stems ca. 2 cm diam.; petioles to 63 cm long, sheathed to 16–28 cm, slender, less than 1 cm diam., the sheath merging imperceptibly with the petiole at the apex; blades trisect, the lobes narrowly confluent at the base, the median lobe oblong-elliptic, acuminate at the apex, cuneate at the base, 27 cm long, 9.3 cm wide, drying pale yellowish brown, matte on the upper surface, slightly paler on the lower surface, the lateral lobes equal to the median lobe, 27–27.5 cm long, 7.5–8 cm wide, very inequilateral, the inner margin narrowly acute, almost paralleling the margin near the base, the outer margin attenuate and acute at the base, not at all auriculate, the lateral lobes markedly inequilateral, oblong-lanceolate, acuminate at the apex, ca. 26 cm long and 8 cm wide, the inner edge narrowly acute at the base, narrowly confluent with the median lobe, the outer edge acute to obtuse, the midrib drying more or less flat on the upper surface, raised beneath; primary lateral veins 3–4 pairs; the tertiary veins weakly visible; the principal collective vein 3–6 mm from the margin. *Inflorescences* 2 per axil, 10–11 cm long, slender; peduncles ca. 7 cm long, drying less than 4 mm diam.; spathe tube oblong-ellipsoid, 2.5–3.5 cm long (dried), 1.1–2.3 cm diam.; spathe blade, whitish, oblong-elliptic, narrowly acuminate at the apex; spadix to 8 cm or longer; pistillate portion of the spadix 7 mm long, 4 mm diam., the stigmas ovoid, 0.6–0.7 mm diam., slightly broader in the direction of the axis, contiguous; staminate portion of the spadix narrowly clavate, ca. 7.5 cm long or more, ca. 7 mm diam., the flowers irregularly 4–6-sided, 1–2 mm diam. (dried), the apex truncate, lacking a medial depression, shallowly incised along the sides between each stamen. *Infructescences* not seen. Fig. 42.

DISTRIBUTION: The species is known only from the type locality in premontane rain forest in Huánuco Department, Peru. It is named in honor of Dr. Alwyn H. Gentry who made the only known collection of the species.

It is distinguished from other South American species by its trisect leaves with the lateral lobes not at all auriculate and equal to the median lobe in length. *Syngonium gentryanum* is probably closest to *S. sparreorum* of western Ecuador. See that species for a discussion of the differences.

The type had a flowering inflorescence in March.

PERU: HUÁNUCO: La Divisora, Tingo María-Pucallpa road near Loreto border, *Gentry et al. 18822* (MO, USM).

20. Syngonium glaucopetiolatum Croat, sp. nov. TYPE: Panama, Chiriquí, E of Boquete along steep forested slopes on Cerro Azul near Quebrada Jaramillo, 1620–1700 m, *Croat 26821* (MO-2272459, holotype).

Caudex haud glaucus, scandens, internodiis 2.5 cm diam.; foliorum petiolus 25–30 cm longus, ad ⅔ longitudinis usque vaginatus; petiolus juvenalis valde glaucus; lamina trisecta; segmentum medium 15–25 cm longum, 11–15 cm latum, ellipticum apice acuminatum; segmenta lateralia 16–24 cm longa, 10–12 cm lata, basi valde inaequalatera, valde auriculata, lateribus exterioribus lateribus, interioribus

FIGURES 37–40.—37. *Syngonium steyermarkii*, *Croat 40842*; adult blade (×1/5).—38. *S. steyermarkii*, *Croat 40842*; pre-adult blade (×1/3).—39. *S. steyermarkii*, *Croat 40842*; adult plant with infructescences (×1/10).—40. *S. angustatum*, *Croat 41699*, adult plant (×1/7).

cuneatis. Inflorescentiae binatae; pedunculus 15 cm longus, valde glaucus; spathae tubus 6–7 cm longus, 5 cm latus, ovatus-ellipticus, valde glaucus.

Hemiepiphytic creeper. Juvenile plants with stems ca. 5 mm diam., the epidermis drying brown, peeling; petioles 9–13 cm long, D-shaped above the sheath, becoming sharply angular on pre-adult and adult plants; blades ovate-triangular, narrowly acute at the apex, mucronate, sagittate at the base, 13 cm long, ca. 5 cm wide at the middle, the posterior lobes 5–5.5 cm long, the posterior lobes soon pinched off and directed outward at 45° angle, noticeably auriculate at the base; intermediate blades with the lateral segments confluent with the medial lobes. Adult plants with stem to 2.5 cm diam. (fresh), shrinking to 1.5 cm diam., the epidermis green, shiny, drying yellowish brown with sharp longitudinal wrinkles; internodes 2–4 cm long; leaves moderately thin, clustered in the upper 30 cm of the stem; petioles 25–30 cm long, sheathed ca. ⅔ their length, the sheath 4–5.5 cm wide when flattened, free-ending and bluntly acute at the apex, the upper part of the petiole subterete with a blunt medial rib; blades trisect, at least sometimes confluent to almost free; median leaflet elliptic, 15–25 cm long, 11–15 cm wide, acuminate at the apex, briefly attenuate at the base; lateral leaflets strongly inequilateral, 16–24 cm long, 10–12 cm wide, the base prominently auricled on the outer margin, cuneate on the inner margin, the midrib bluntly depressed above, prominently raised beneath, the primary lateral veins and the principal collective vein weakly sunken above, raised beneath, the tertiary veins clearly visible (on dried specimens); primary lateral veins 6–8 pairs, mostly departing midrib at ca. 40° angle; collective vein ca. 12–18 mm from the margin (midway to the apex). *Inflorescences* 2 per axil; not seen in flower. *Infructescences* pendent; peduncle to 15 cm long; peduncle and spathe tube pruinose; spathe tube ovoid-ellipsoid, 6–7 cm long, ca. 5 cm diam. (fresh); spathe blade (dried) brown, subcoriaceous, ca. 10 cm long, acuminate at the apex, sometimes persisting in its dried condition; mature fruits not seen. Figs. 43, 47.

DISTRIBUTION: *Syngonium glaucopetiolatum* is known from Costa Rica where I have seen it at Monteverde (Guanacaste) and Panama in what is believed to be lower montane wet forest at elevations of 1300–1800 m.

It is distinguished by its large 3-lobed blades with markedly auriculate lateral lobes and by its glaucous young petioles, peduncles, and spathe tubes. The blade shape of *S. glaucopetiolatum* approaches that of *S. mauroanum* but that species has been found to range no higher than 450 m and is apparently restricted to premontane moist forest.

The species presumably flowers early in the rainy season, perhaps in June, because immature fruits have been seen in August and fruits of mature size have been seen in February.

PANAMA: CHIRIQUÍ: East of Boquete, *Croat 26821* (MO).

21. Syngonium harlingianum Croat, sp. nov. TYPE: Ecuador, Pastaza, Mera, Pantanos, 1100 m, *Harling 11064* (GB, holotype).

Planta terristris, caudex ca. 1 cm diam.; lamina simplex trilobata, lobi conjuncti, lobus medius 7.5–10.5 cm longus, 2.7–6 cm latus, lobi laterales inaequilaterae conspicuae auriculatae. Inflorescentia solitaria, 9.5 cm longa, spatha 11.5 cm longa, tubo 4.5 cm longo, ca. 2 cm lato, viridi, lamina luteola, acuminata; spadix 8.5 cm longa, parte feminea spadicis ca. 2 cm longa.

Terrestrial. Adult plants with stems ca. 1 cm diam.; internodes 1–2 cm long near the apex; petioles 12–14 cm long, sheathed ca. ⅔ their length, the free portion subterete, ca. 2 mm diam., the sheath merging almost imperceptibly with the petiole at its apex; blades 3-lobed, drying yellowish green, the median lobe oblong-elliptic, acuminate to obtuse at the apex, narrowed at the base and confluent with the lateral lobes, 7.5–10.5 cm long, 2.7–6 cm wide, the lateral lobes markedly inequilateral (the inner part ½ or less as wide as the outer part), more or less elliptic, obtuse to acute at the apex, 5.5–8 cm long, 2–4 cm wide, rounded or more commonly auriculate on the outer edge at base, the midrib naked for 5–10 mm, the auricles to 2.5 cm long, rounded or oblong, not at all constricted at the base, the surfaces drying matte, yellowish green, slightly paler beneath; midrib drying flat on upper surface, weakly raised beneath with obscure scabrid lines; primary lateral veins 2–4 pairs; tertiary and quaternary veins distinctly visible; primary collective vein arising from the first or second primary lateral vein, 2–4 mm from the margin. *Inflorescences* solitary; peduncle 9.5 cm long, ca. 3 mm diam. (dried); spathe 11.5 cm long; spathe tube green, narrowly ellipsoid, 4.5 cm long, ca. 2 cm diam.; spathe blade narrowly elliptic, membranous, yellowish, acuminate at the apex; spadix 8.5 cm long; pistillate portion of the spadix ca. 2 cm long, ca. 5 mm diam., the flowers contiguous, ca. 1 mm diam.; sterile staminate flowers irregularly elongated in the direction of the axis, 3–3.5 mm long in direction of the axis, 1–1.6 mm wide perpendicular to axis; staminate portion of the spadix cylindroid, narrowly tapered toward the apex, drying ca. 1 cm diam., the flowers mostly rhombic, the apex truncate, matte, the margin crenate, not at all incised between the anthers. *Infructescences* not seen. Fig. 44.

DISTRIBUTION: *Syngonium harlingianum* is known only from the type collection and is named in honor of its collector, Dr. Gunnar Harling, one of the coauthors of the *Flora of Ecuador*.

The species is not closely related to any other species nor is it confused with any other species. It is characterized by its small, 3-lobed leaves with confluent leaflets. It was described by its collector as being terrestrial, an unusual condition in the genus. While it is not unusual to find juvenile and pre-adult leaves on the ground, I have never found adult plants in other than an epiphytic or hemiepiphytic situation.

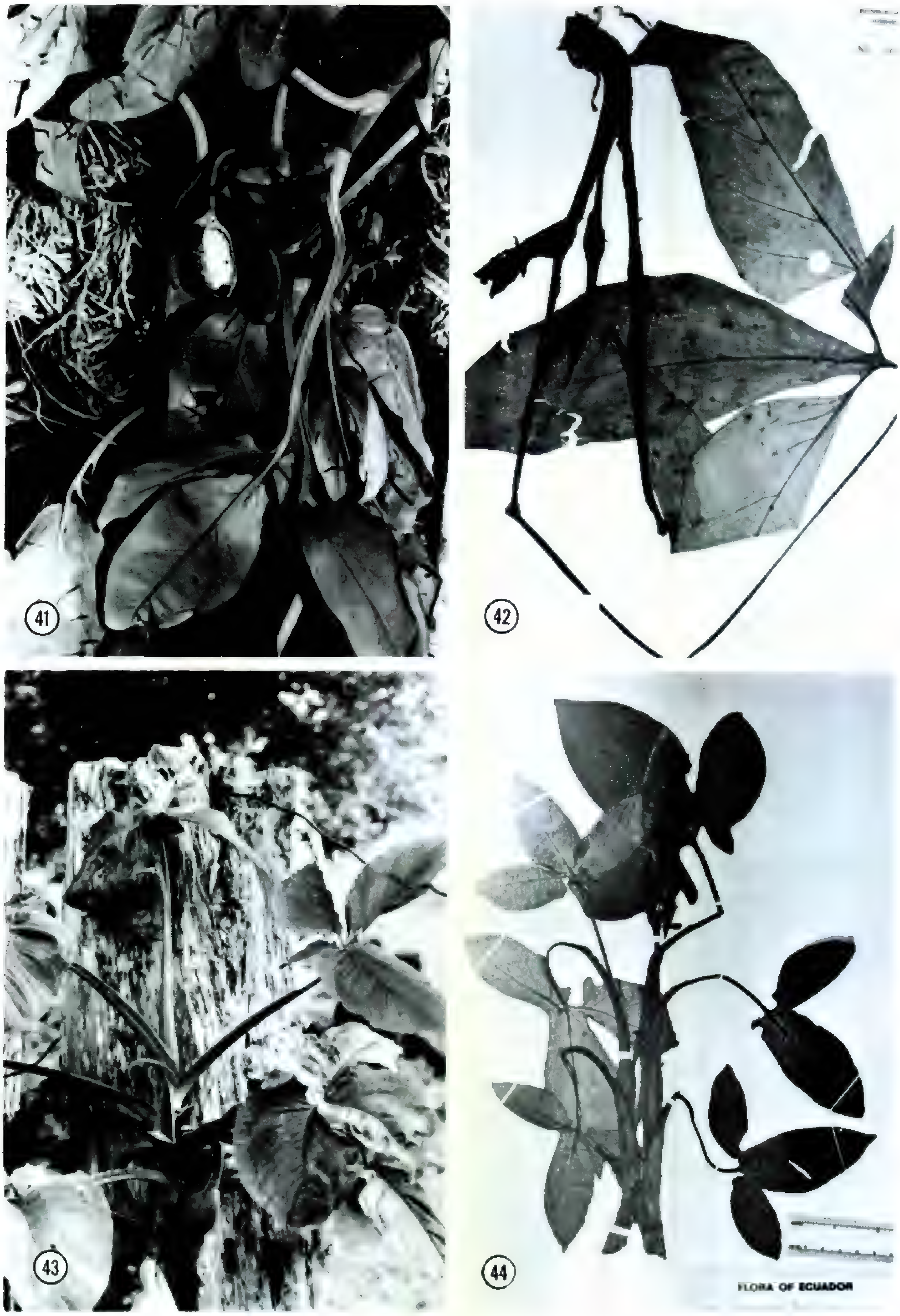
The type collection was in flower in late February.

ECUADOR: PASTAZA: Mera, *Harling 11064* (GB).

22. **Syngonium hoffmannii** Schott, Oesterr. Bot. Z. 8:178. 1858. TYPE: Costa Rica, Alajuela, Candelaria, Alto de Sta. Cruz (presumably the modern day Candelaria southeast of San Ramón and Palmares at ca. 1000 m) *Hoffmann s.n.* (not seen) (Schott drawing of the Hoffmann collections, Schott Aroideae #3212 was seen).

Porphyrospatha hoffmannii (Schott) Engler in A. DC., Monogr. Phan. 2:291. 1879.

Juvenile plants with glaucous stems; internodes 1–4 cm long, 3–6 mm diam.; petioles sheathed ½–⅔ their length; blades sagittate, 4–13 cm long, medium green or with grayish white midrib and primary lateral veins (fide Birdsey, 1955), all



FIGURES 41–44.—41. *Syngonium erythrophyllum, Croat 11778*; adult plant with mature-sized infructescences ($\times 1/5$).—42. *S. gentryanum, Gentry et al. 18822*; adult plant with inflorescence.—43. *S. glaucopetiolatum, Croat 26821*; adult plant with infructescences ($\times 1/8$).—44. *S. harlingianum, Harling 11064*; adult plant with inflorescence.

the major veins sunken above, raised beneath, the anterior lobe 4–18 cm long, ovate-deltoid, slightly or not at all constricted at the base, acute to acuminate and apiculate at the apex, the posterior lobes 2.5–9 cm long, acute to acuminate at the apex; intermediate leaves with the lateral lobes only slightly inequilateral or very inequilateral but lacking a conspicuous, protruded auricle. Adult plants with stems sometimes glaucous, usually 1–2 cm wide; internodes weakly sulcate above the petioles, 1.5–10 cm long on flowering branches, olive green, drying brown, flaky, often weakly and rather sparsely muricate; petioles sometimes glaucous, paler than the stems, 12–33 cm long, sheathed $^2/_3$–$^4/_5$ their length, subterete above the sheath, somewhat flattened laterally, sharply to bluntly 1-ribbed adaxially; blades trisect (or rarely sub-5-sect); leaflets free to confluent, 9–28 cm long, 3.5–11 cm wide, the upper surface medium green, semiglossy, the lower surface only slightly paler; median leaflet oblong-elliptic to ovate-oblong or lanceolate, equal or more frequently unequal, acuminate at the apex, obtuse to acute or attenuate at the base; lateral leaflets 6–24 cm long, 2–8 cm wide, very unequal, acute on the inner margin at the base, usually prominently auriculate on the outer margin at the base, the auricles directed downward and in line with the leaflet or directed somewhat outward, usually ± parallel with the petiole, strongly to not at all pinched off from the leaflet (rarely appearing as another leaflet); primary lateral veins 5–10 pairs, sunken on the upper surface, raised beneath, the minor veins obscure on the upper surface. *Inflorescences* usually 1–3 (less frequently to 4 in Panama) per axil; peduncles sometimes glaucous (commonly glaucous at higher elevations), 3–9 cm long and erect at anthesis, 6–13 cm long and pendent in fruit; spathe tube broadly ovoid to ovoid-ellipsoid, dark green outside, becoming tinged with purple in age, red to violet purple within, 4–4.5 cm long, 2–2.5 cm diam.; spathe blade broadly ovate, greenish white to white, cuspidate at the apex, 5.5–8 cm long, 4.8–5.5 cm wide; pistillate portion of the spadix greenish, 2–2.5 cm long, tapered gradually toward the apex, 1.2–1.6 cm diam., the flowers 2-carpellate, the stigma 2-lobed, circular, the syncarp 3–4 mm diam. at the apex; staminate portion of the spadix white, 5.5–9 cm long, 1.4–1.7 cm diam., broadest at about the middle, only slightly constricted at the point of merger with the sterile staminate flowers, then slightly broader toward the base, the fertile staminate flowers regularly to irregularly 4-lobed, the sterile staminate flowers slightly larger, irregular, closely compacted. *Infructescences* usually oblong-ellipsoid (sometimes ellipsoid), green heavily tinged with purple or sometimes yellowish (fide herbarium labels), 6–10 cm long, 3–4.5 cm wide; syncarp white, to 5.5 cm long and 3.5 cm diameter. Figs. 48, 49, 53.

DISTRIBUTION: *Syngonium hoffmannii* ranges from northern Costa Rica to Cerro Pirre in eastern Panama. It usually occurs in lower montane rain forest but is also frequent in premontane rain forest and tropical wet forest. It has also been collected, though much less frequently, in premontane wet forest.

The species is an extremely variable one and might eventually prove to consist of more than one element. Altitudinal range is particularly great ranging from 300 m to 1800 m. The greatest differences are exhibited in the degree of lobing of the lateral leaflets, in the shape and coloration of the infructescences, and in the degree to which petioles and inflorescences are glaucous. More Costa Rican and Panamanian collections at higher elevations were reported to have glaucous parts.

FIGURES 45–48.—45. *Syngonium angustatum*, *Croat 41699*; inflorescence after 2nd day of flowering with the spathe blade and staminate portion of the spadix withering. (×2/5).—46. *S. erythrophyllum*, *Croat 14955*; adult plant with inflorescence at anthesis (×1/4).—47. *S. glaucopetiolatum*, *Croat 26821*; stem and infructescences (×2/7).—48. *S. hoffmannii*, *Croat 33508b*; adult blades (×1/5).

The species might be confused in Costa Rica with *S. wendlandii* which has similar leaves. See that species for a discussion of the differences.

Flowers have been found in March, May, and December. Fruits are most common from July to September but have been seen immature from December to August.

COSTA RICA: ALAJUELA: NNE of Bijagua, *Burger & Baker 9850, Croat 36268, 36270, 36515* (MO); NW of Zarcero, *Croat 43532, 43575, 43627* (MO). CARTAGO: E of Cachí, *Croat 47084* (MO); Between town of Jicotea and Río Pacuare, *Croat 36558* (MO); SE of Platanillo, *Croat 36731* (MO). HEREDIA: Near Cariblanco, *Croat 35653* (MO); San José de la Montaña, *Echeverria 4077* (F); N of Vara Blanca, *Croat 35594, 35619* (MO). PUNTARENAS: N of La Unión, *Croat 26686* (MO); Monteverde, *Jiménez s.n.* (MO). SAN JOSÉ: Santa María de Dota, *Standley 42097, Standley & Valerio 43322* (US).

PANAMA: CHIRIQUÍ: Vicinity of Cerro Colorado and Escopeta, *Croat 33508, 48441* (MO); Fortuna Dam Site, *Croat 48669, 48722, 48804, 49885, 50025* (MO); Las Lagunas near Volcán, *Folsom & Page 5979* (MO); Monte Rey above Boquete, *Croat et al. 15667* (MO). COCLÉ: La Mesa above El Valle de Antón, *Croat 37341A* (MO); Alto Calvario above El Copé, *Croat 49201, 49207* (MO). COLÓN: E of Santa Rita Ridge, *Correa & Dressler 637* (SCZ), *Croat 13893, 34351* (MO). DARIÉN: Summit of Cerro Pirre, *Gentry & Clewell 7027* (MO); Vicinity Río Tuquesa, *Croat 27180* (MO). HERRERA: Above Chepo de las Minas, *Folsom, Channell & Small 7009* (MO). PANAMÁ: Cerro Azul, *Croat 17268* (MO), *Dwyer 4100* (MO), *Tyson & Blum 4100* (SCZ); Cerro Campana, *Croat 12075, 14226, 25251, 35948, 35962, Porter et al. 4215* (MO), *4262* (MO, US); Vicinity Cerro Jefe, *Croat 35921* (MO), *Lewis et al. 226* (F, GH, K, MO, NY, UC, US), *Tyson et al. 3354* (SCZ); *Wilbur et al. 15572* (MO); El Llano-Cartí Road, *Croat 33776, 34805A, Mori & Kallunki 4092* (MO); Vicinity Finca Neptuno, *Nee 11534* (MO); Vicinity of La Eneida, *Luteyn & Kennedy 1755* (DUKE, MO). VERAGUAS: Between Alto Piedra and Calovebra, *Croat 27391* (MO); N slope of Cerro Alto Higo (El Montoso), *Hammel 4267* (MO); Along Río Primero Braso, *Croat 25970, Liesner 827* (MO); Vicinity of Santa Fe and Río Calovebra, *Croat & Folsom 33986, Croat 34195, 34231, 48888, 48889* (MO); Beyond Tres Brazos River, *Croat 25647* (MO).

23. Syngonium laterinervium Croat, sp. nov. TYPE: Costa Rica, Puntarenas, Osa Peninsula, Corcovado National Park within 2 km of park headquarters at Sirena, below 200 m, 8°29′N, 83°36′W, *Liesner 2951* (MO-2588405, holotype).

Caudex scandens haud glaucus, internodiis 2–8 cm longis, 5–10 mm diam.; foliorum petiolus 10–20 cm longus, vaginatus praeter 1–3 cm distale, lamina trisecta, segmentum medium oblongum-ellipticum, leviter inaequalaterum, (5.5–)8–17 cm longum, 2.3–5.5 cm latum, apice acuminatum, mucronulatum, basi acutum ad attenuatum, segmenta lateralia (5.2–)9–14 cm longa, 2.5–4 cm lata, oblonga-elliptica, inaequalatera basi auriculata; folia venis lateralibus utroque latere 4–6, nervis parvis vix prominioribus, subangulo ca. 10–20°. Inflorescentia pedunculo 4.5 cm longo, in axilla solitarius; spathae tubus ca. 3.5 cm longus, 1.2 cm diam., anguste ellipticus, extus viridis pallidus; spathae lamina ca. 5 cm longa, alba.

Juvenile stages not seen. Adult plants with scandent stems, much branched; internodes 2–8 cm long, 5–10 mm wide, green, drying light brown, the periderm often flaky in small patches; petioles 10–20 cm long, sheathed except for the last 1–3 cm, the sheath free-ending and narrowly acute at the apex, those subtending inflorescences much broader in the lower half, the portion between the petiole and blade flattened adaxially; blades trisect, the leaflets overlapping or not distinctly free from one another; median leaflet oblong-elliptic, somewhat inequilateral, acute and cuspidate to narrowly acuminate at the apex, obtusely cuneate to attenuate at the base, (5.5–)8–17 cm long, 2.3–5.5 cm wide; lateral leaflets oblong-elliptic, very inequilateral, narrowly acute to attenuate on the inner margins at the base, conspicuously auriculate on the outer margins at the base, usually joining the petiolule at ca. 90° angle, the petiolule 4–10 mm long, canaliculate on upper side, the margin continuous with the margin of both the median and lateral

leaflets, the auricles about as long as or longer than broad, 12–28 cm long, oblong to triangular, rounded at the apex; midrib weakly sunken on upper surface, raised beneath; primary lateral veins 4–6 pairs, slightly more conspicuous than the smaller lateral veins, all the veins below clearly visible, departing the midrib at ca. 70° angle, spreading almost straight to the collective vein; collective veins 2 or 3, the principal one 2–5 mm from the margin. *Inflorescences* solitary; peduncle ca. 4.5 cm long, ca. 3 mm diam., erect at anthesis; spathe ca. 8.5 cm long, spathe tube narrowly ellipsoid, ca. 3.5 cm long, 1.2 cm diam., the outside pale green; spathe blade elliptic, ca. 5 cm long, acuminate at the apex, white; spadix ca. 7 cm long; pistillate portion of the spadix 1.8 cm long, ca. 9 mm diam., the flowers irregularly hexagonal, the stigmas flat at the apex, 1.5–2 mm diam.; staminate portion of the spadix ca. 5 cm long, clavate, ca. 1.5 cm diam. at the broadest point in the upper ⅓, the fertile staminate flowers mostly rhombic to sometimes irregularly hexagonal at the apex, the surface minutely rugose, the margins weakly crenate. *Infructescences* unknown. Fig. 16.

DISTRIBUTION: *Syngonium laterinervium* is known from southwestern Costa Rica and northwestern Panama in tropical wet forest life zones in the region surrounding Golfo Dulce, at elevations ranging from near sea level to 450 m.

It is most easily confused with *S. hoffmannii* but differs in having the lateral veins departing the midrib at no less than ca. 70° angle and in having the primary lateral veins only slightly more prominent than the lesser lateral venation. *Syngonium hoffmannii* has at least the lower primary lateral veins departing the midrib at a much sharper angle (ca. 50°), and much more conspicuous than the minor lateral veins (drying much darker than the surface).

The species was first collected by Paul Allen in 1951 and was not collected again until 1973. According to *Allen 6035* the plant was a branching vine forming dense masses on the trunks of large trees in climax forest.

Flowers have been found in July.

COSTA RICA: PUNTARENAS: Corcovado National Park, *Liesner 2951* (MO); Esquinas Forest, *Allen 6035* (F, GH, US).
PANAMA: CHIRIQUÍ: West of Puerto Armuelles, *Busey 605* (MO).

24. Syngonium macrophyllum Engler, Pflanzenr. IV. 23E (Heft 71):128. 1920. TYPE: Mexico (locality not known) (B, holotype, two specimens made from cultivated plants in Berlin).

Juvenile plants with glaucous stems (at least in the northern extreme of its range); petioles 7–25 cm long, sheathed ca. ½ their length; blades subcoriaceous, broadly ovate, 8–16 cm long, 6–10 cm wide, the posterior lobes at first rounded, becoming sagittate, rounded at the apex; intermediate leaves with the apical lobe elliptic, acuminate at the apex, much constricted at the base, the posterior lobes becoming nearly pinched off, narrowly rounded to acute at the apex. Adult plants with stems glaucous (or possibly not in Panama) 3–4 cm diam., usually not branched and appressed to trees; internodes 1–4 cm long near the apex; petioles often glaucous, 25–60 cm long, sheathed ½–¾ their length with a weak to prominent rib between the sheath and the blade, the sheath free-ending and acute at the apex; blades subcoriaceous, pedatisect; leaflets 7–9, mostly free or the outer

ones confluent, the lowermost usually variously auriculate, this soon pinched off to form a leaflet, dark to medium green on the upper surface, smooth, the lower surface light green; rachis sharply margined; median leaflet oblanceolate, elliptic, broadly elliptic or ovate-elliptic, acuminate to acute and down-turned at the apex, cuneate to abruptly attenuate at the base, 17–47 cm long, 5–18 cm wide; primary lateral veins 3 or 4 pairs in the median leaflet, weakly sunken above, raised below. *Inflorescences* 4–8 per axil; peduncles almost terete, glaucous in the northern part of the range, erect, 10–13 cm long at anthesis, 14–20 cm diam. and pendent in fruit; spathe tube ovate, green and glaucous outside, green to greenish tan inside, 3–5.5 cm long, 3–5 cm diam.; spathe blade 7–11.5 cm long, at first green, becoming cream, mucronate at the apex; pistillate portion of the spadix 1.5–3 cm long, ca. 2 cm diam. at the base, tapered to the apex, to 1.5 cm diam. at the apex, pale green, the flowers irregularly 5–6-sided, the stigma subsessile, discoid, yellowish at anthesis; staminate portion of the spadix oblong-ellipsoid, abruptly constricted just above the sterile staminate flowers, the fertile staminate flowers with 4 stamens, the synandrium with the line of fusion scarcely visible, the apex truncate or with a conspicuous central depression, the sterile staminate flowers somewhat larger. *Infructescences* often rather massive, 8–14 cm long, 5–8 cm wide, yellow and pruinose in the northern part of the range; syncarp narrowly ovoid to subglobular, 6–10 cm long, 3.5–6 cm wide, brown; mesocarp sweet smelling, fleshy; seeds obovoid, white before maturity, becoming dark gray, 1.4–1.8 cm long, ca. 1.5 cm wide. According to natives in Guatemala near Puerto Barrios, the spathe tube of the mature infructescence turns yellow, whereas in Panama immature fruits have been seen turning a pale brick red. Figs. 50, 51, 54–56, 61.

DISTRIBUTION: *Syngonium macrophyllum* ranges from Mexico to Ecuador (Pacific slope only). Collections from Río Palenque Field Station reported by Dodson & Gentry (1978) as *S. podophyllum* are also this species. I believe the latter species is restricted to the other side of the Andes.The species is known from wetter parts of tropical moist forest, premontane wet forest and tropical wet forest and ranges from sea level to 1100 m. It is most common below 700 m. In Panama the species is always found in good forest or along roads recently opened. While this is usually the case also in the remainder of its range, to the north one finds the plants frequently in more disturbed areas. However, in most cases it is possible that plants could have persisted in the areas where they were collected from earlier forest disturbances.

It is possible that the Panamanian plants from central Panama (chiefly west of the Isthmus on Santa Rita Ridge, the Pipeline Road, El Llano-Cartí Road, etc.) represent a distinct species. These collections (e.g., *Croat 13952*) differ in having only a few primary lateral veins, mostly restricted to the basal half of the blade. Panamanian plants do not have glaucous parts and tend to have somewhat smaller leaves with narrower segments than do collections made from the northern part of the range.

Syngonium macrophyllum is not usually confused with any other species and is distinguished by its large parts, smooth, subcoriaceous, 7–9-pedatisect leaves and by its ovate-cordate juvenile blades. It may be confused with *S. podophyllum*

FIGURES 49–52.—49. *Syngonium hoffmannii, Croat 33508*; preadult blades (×1/5).—50. *S. macrophyllum, Croat 36339*; pre-adult blades (×1/8).—51. *S. macrophyllum, Croat 40140*; juvenile stems and blades (×1/3).—52. *S. mauroanum, Bartlett & Lasser 16708*; adult blades showing the usual 3-lobed and the rare 5-lobed blades.

in some parts of Panama and Costa Rica where they both occur in wetter parts of tropical moist or premontane wet forests.

Flowers and fruits are found throughout the year but principally from June to August.

Colombia: chocó: E of Quibdo, *Forero & Jaramillo 2637* (COL); Valley of Río San Juan near Docordo, *Forero et al. 4351, 4546* (MO); E of Yuto, *Gentry & Renteria 24372* (MO).

Costa Rica: alajuela: Vicinity of Laguna Hule, *Luteyn 3228* (DUKE, MO); Between Cañas and Upala, *Burger & Baker 9883* (F), *Croat 36332, 36339, 36400, 36479, 36491* (MO). heredia: Near Puerto Viejo, *Croat 35721* (MO); S of Hone Creek on road to Bribri, *Croat 43183* (MO).

Ecuador: No other location, *Eggers 15131*, (F, GH, NY, US). esmeraldas: S of Esmeraldas, *Sparre 15498* (S); San Lorenzo, *Jativa & Epling 724* (NY, UC), *738, 830* (UC). guayas: Vicinity of Naranjito, *Camp E-3584C, 3584B* (NY). imbabura: Between Ibarra and Lita, *Croat 38917* (MO). los ríos: Río Palenque Field Station, *Croat 38677* (F, MO), *Gentry 9986* (MO); Between Babahoyo and Montalve, *Sparre 17961* (S). pichincha: Santo Domingo Alluriquín, *Sparre 14790* (S).

Guatemala: alta verapaz: Between Campur and Socoyo, *Croat & Folsom 33986* (F, MO), *Standley 91929* (F); Cubilquitz, *Steyermark 44397* (F); Pantín, *Standley 70551* (F). izabal: Near Entre Ríos, *Standley 72782* (F); S of Puerto Barrios, *Croat 41805* (MO).

Honduras: atlantida: Lancetilla Valley, *Chickering 82, 160* (MICH). copán: E of Copán, *Croat 42528* (MO).

Mexico: chiapas: N of Isthuatán, *Croat 47867* (MO); SE of Palenque, *Croat 40140* (MO).

Nicaragua: chontales: Above Cuapa, *Stevens 3665* (MO). zelaya: Along Caño Majagua, *Stevens 6997* (MO); SW of Colonia Naciones Unidas, *Stevens 4985* (MO); Road to Colonia Yolania and Colonia La Esperanza, *Stevens 6372* (MO); Road to Panua, *Stevens 7797* (MO); Road from Siuna to Matagalpa, *Stevens 7458* (MO).

Panama: bocas del toro: Road between Almirante and Ojo del Agua, *Croat 38217* (MO); Forest above Milla 7.5, *Croat & Porter 16242* (MO). canal zone: Pipeline Road, *Croat 16699* (MO, SCZ). colón: Santa Rita Ridge Road, *Croat 34352* (MO); Between Tonosí and Río Indio, *Croat 33534* (MO). darién: Santa Fe, *Duke 14259* (MO). panamá: Vicinity of Cerro Campana, *Croat 35964* (MO); El Llano-Cartí Road, *Croat 25187* (AAU, MO, PMA); Logging roads along Río Pita, *Duke 4746* (BH, GH, MO, US). san blas: Río Acla, *Sugden 625* (MO).

25. **Syngonium mauroanum** Birdsey ex Bunting, Baileya 14:18. 1966. type: Panama (exact locality unknown, cultivated at Amazon Gardens, Miami, Florida) *Bunting 1441* (BH, holotype).

Juvenile plants with stems at first short, forming rosettes, becoming elongate, green; petioles 6–13 cm long, sheathed to the middle or somewhat above the middle, sharply 1-ribbed from the sheath to the blade; blades sagittate, the primary lateral veins and many secondary veins sunken above and beneath, the upper surface marked along the midrib and sometimes along the larger lateral veins with a discolorous band of gray or yellowish green, the anterior lobe ovate, acuminate, 5–16 cm long, the posterior lobes triangular to ovate, acute to rounded at the apex, 2–10 cm long. Adult plants with stems not glaucous, scandent, appressed to trees; internodes 1–12 cm long, 1–1.5 cm wide; petioles sheathed ½–¾ their length; blades thin, subtrisect to usually trisect, rarely 5-segmented, medium green, matte above, slightly paler and matte beneath; leaflets free or sometimes confluent; median leaflet elliptic to ovate-elliptic, 12–21(–30) cm long, 3.5–10(–12) cm wide, acuminate at the apex, obtuse to acute and attenuate at the base, the margin minutely undulate and sometimes appearing toothed on drying; lateral leaflets inequilateral, sometimes auriculate, the auricle usually conspicuously hastate, narrowly rounded at the apex; primary lateral veins 6–10 pairs, distributed throughout the blade (but thicker in the lower half of the blade), conspicuously sunken above, raised beneath; principal, secondary, tertiary and some quaternary veins sunken above, raised beneath, the reticulate veins clearly

FIGURES 53–56.—53. *Syngonium hoffmannii*, *Croat 26686*; adult plants with infructescences (×1/3).—54. *S. macrophyllum*, *Croat 16699*; immature infructescence with spathe removed (left) and inflorescence with spathe removed (right) (×1).—55. *S. macrophyllum*, *Croat 41805*; inflorescence at anthesis with hole cut in spathe tube (×½).—56. *S. macrophyllum*, *Croat 42528*; adult plant with infructescences (×1/20).

visible beneath. *Inflorescences* 1 or 2 per axil; peduncles 3.5–9 cm long and erect at anthesis, 8–14 cm long and pendent in fruit; spathe tube ellipsoid to narrowly ovoid, 3.5–5 cm long, 1.5–2.5 cm diam., green outside, dark violet purple inside; spathe blade ovate-elliptic, 6–8 cm long, 4–5 cm wide, acuminate, white; spadix 6.5–10 cm long, narrowly clavate; pistillate portion of the spadix ca. 1 cm long on the back side, ca. 1.5 cm long on the front side, the flowers irregularly rhombic at the apex, 2.3–3 mm diam., the stigma ca. 1.2 mm diam.; staminate portion of the spadix white, the sterile part ca. 1.5 cm long, the fertile part 5–6 cm long, the synandrium irregularly rounded to rhombic at the apex, the margin irregular, the apex not drying smooth, irregularly undulate. *Infructescences* 4.5–7.5 cm diam., red on the outside, violet purple within; syncarp brown, 4.5–6 cm long, 2.5–4 cm diam.; mesocarp white; seeds ovoid, 5–6 mm long, 4–5 mm diam., dark brown. Figs. 52, 57, 58.

DISTRIBUTION: *Syngonium mauroanum* is known from Costa Rica and Panama in seasonally dry parts of tropical moist forest and especially from premontane moist forest life zones. It is an interesting testimony to the apparent accuracy of the Holdridge Life Zone Maps that the only collection from Costa Rica was also found in a narrow band of premontane moist forest in Guanacaste and that the species has been collected in the small isolated patch of premontane moist forest around Santa Fe in Veraguas. The species ranges from sea level to about 450 m elevation.

The species can be recognized by its usually hastate-lobed blades with distinctive prominent venation. It is not easily confused with any other species because of its relative isolation and narrow ecological range, but the species is closest to *S. standleyanum*, a species from premontane wet forest in Guanacaste Province, Costa Rica. That species often shows no sign of auricles on the lateral leaflets (a feature rarely exhibited by *S. mauroanum*) and has a densely papillate stem. *Syngonium standleyanum* may ultimately prove to be merely an ecological variant of this species.

Flowers are known from April to June and immature fruits in November and January.

COSTA RICA: PUNTARENAS: N Puntarenas, *Janzen 10731* (MO); Ujarrás de Buenos Aires, *Pittier 11121* (US).

PANAMA: CHIRIQUÍ: Near Remédios, *Woodson et al. 1189* (F, GH, MO). HERRERA: S of Ocú, *Lewis et al. 1637* (GH, US). LOS SANTOS: Vicinity of Tonosí, *Croat 9763* (MO), *Lewis et al. 1561* (GH, K, US), *Lewis et al. 2193* (MO), *Tyson et al. 2954* (MO, SCZ). PANAMÁ: Vicinity of Panama City, *Bartlett & Lasser 16708* (DUKE, MICH, MO). VERAGUAS: Vicinity Santa Fe, *Croat 27345, 34249* (MO); E edge of Escuela Agrícola Alto Piedra, *Croat & Folsom 33981* (MO); Vicinity of Santa Fe, *Nee 8038* (GH, MO), *Luteyn 4048* (DUKE, MO); S of Santiago, *Nee 8231* (MO), *Tyson 6045* (SCZ).

26. Syngonium neglectum Schott, Bonplandia 7:163. 1859. TYPE: Mexico, Veracruz, near El Mirador (at Km 45 on road from Puente Nacional to Huatusco, 21 Km E of Huatusco), *Liebmann s.n.* (C) (type photo of Schott drawing 3212, NYBG 4315).

S. auritum (L.) Schott var. *neglectum* (Schott) Engler ex A. DC., Monogr. Phan. 2:294. 1879.

S. morelosense Matuda, Anales Inst. Biol. Univ. Nac. México 22:369. 1951[1952]. TYPE: Mexico, Morelos, Río Pollo near Cuernavaca, ca. 1500 m, *Matuda 25933* [MEXU, isotype; according to Birdsey (1955), the holotype originally designated by Matuda was lost in the mail].

S. occidentale Bunting, Gentes Herb. 9:370. TYPE: Mexico, Nayarit, at Km 15 on road from Tepic to Jalcocotán, 900 m, *Moore & Bunting 8708* (BH, holotype; MEXU, US, isotypes).

Juvenile plants with stems not glaucous; petioles sheathed ²/₃–⁴/₅ their length, 8–30 cm long; blades subsagittate to hastate, the anterior lobe ovate, acuminate at the apex, 9–14 cm long, 6–9 cm wide, the posterior lobes very unequal, to 10 cm long and 4 cm wide; intermediate blades with the posterior lobes increasingly pinched off, 3-lobed with conspicuous, broad auricles. Adult plants with stems not glaucous, 1.5–2.5 cm diam., shiny, olive green, becoming tan, short or elongated-creeping and firmly attached to trees; sap pale tan, copious; internodes 1.5–10 cm long on flowering parts, longer below, green when fresh, drying pale brown with many longitudinal folds; petioles 17–55 cm long, semiglossy, sometimes glaucous, slightly paler than the stem, sheathed ¹/₂–⁴/₅ their length, the sheath free ending at the apex (the free ending portion sometimes to 2.5 cm long), the portion between the sheath and the blade subterete, obtusely angled adaxially; blade firm, semiglossy, weakly coriaceous, sometimes semiglaucous on the upper surface, usually pedatisect with 3–7 leaflets, occasionally 9, rarely 11; leaflets usually free or sometimes (especially the outer leaflets) confluent; median leaflet ovate to elliptic, rarely suborbicular, 14–38 cm long, 5–25 cm wide, acuminate at the apex with a small apiculum, obtuse to rounded and attenuate at the base, somewhat inequilateral; outermost leaflets often with slender, almost oblong auricles (these eventually pinching off and becoming widely separated as distinct leaflets); primary lateral veins 5–13 pairs, sunken above, prominently raised beneath; tertiary veins clearly visible on the lower surface. *Inflorescences* 1–3, usually 1; peduncles 7–15 cm long and erect at anthesis, 12–18 cm long and pendent in fruit; spathe tube suborbicular to ellipsoid, 4.5–6.5(–8) cm long, 4–6 cm diam., green outside, dark dull waxy red or sometimes violet purple inside; spathe blade orbicular to elliptic, acuminate at the apex, green becoming yellowish cream within (sometimes reddish at the base), sometimes creamy white on both sides, reflexed from the spadix at maturity, 9–15 cm long, 7–14 cm wide (when flattened); spadix sometimes curved sharply outward somewhat above the pistillate portion; pistillate portion of the spadix 1.4–3.9 cm long, 1.5–2.9 cm diam., yellowish green, the flowers 2(–3)-carpellate, the stigma bilobed; staminate portion of the spadix white, curved forward, 8–16 cm long, 1.5–3 cm diam., the flowers usually 4-androus (rarely more), the synandrium usually flat at the apex, usually irregularly 6-sided, ca. 5 mm long, 3 mm wide, the margins weakly sinuate. *Infructescences* orange to red, 6–9 cm long, 5–7 cm diam.; fruiting spadix brown, 5–7 cm long, 3–5 cm diam.; mesocarp fleshy, white; seeds grayish black to dark black, 6–10 mm long, 5–7 mm wide (Birdsey reports them as 10–13 mm long by 6–9 mm wide). Figs. 59, 60, 62, 63.

DISTRIBUTION: *Syngonium neglectum* is known only from Mexico but is widespread in that country, ranging from Tamaulipas to Chiapas on the Atlantic slope and from Nayarit to Chiapas on the Pacific slope. The range of life zones is uncertain, but the species is obviously quite variable ecologically and has been collected in both relatively dry and relatively wet areas. The species is most common at higher elevations in relatively dry situations. It occurs from near sea level (in the north of its range) or from near 350 m (in the south of its range) to 1700 m elevation.

The species was considered a variety of *S. auritum* (a strictly West Indian species) by Engler & Krause (1920). *Syngonium auritum* is distinguished by a spathe blade twice as long as the staminate portion of the spadix, whereas in *S. neglectum* the spathe blade and staminate portion of the spadix are of nearly equal length. Other characters which help to distinguish *S. neglectum* are the usually solitary inflorescences, and, especially, the size of the spathe and the staminate portion of the spadix, both of which are larger than for any other species.

Syngonium neglectum can be confused vegetatively with *S. podophyllum* where they occur together, although the latter species does not occur on the Pacific slope in Mexico and usually occurs at lower elevations, whereas *S. neglectum* frequently ranges above 1000 m. *Syngonium neglectum* also lacks the glaucous stems usually present on Mexican plants of *S. podophyllum*.

Syngonium neglectum apparently flowers during the first half of the rainy season (June to September) and also at the beginning of the dry season.

MEXICO: CHIAPAS: E of Bochil, *Ton 2577* (DS, F, MEXU, MICH); Between Chiapilla and San Lucas, *Laughlin 278* (DS); Escuintla, *Croat 43864* (MO), *Matuda 20947* (MEXU), *17284* (F, MEXU); N of Ocozocoautla, *Breedlove 25214* (DS), *Croat 40586* (MO); Between Palenque and Bonampak, *Croat 40220* (MO); NW of Solusi, *Lathrop 6560* (DS). DISTRITO FEDERAL: Tamasopo near Agua Buena, *Rzedowski 10708* (MEXU). GUERRERO: Below Tierra Colorada on road to Acapulco, *Moore & Bunting 8841* (BH). HIDALGO: Puerto del Zopilote, *Moore 2708* (BH, GH); S of Tamazunchale, *Barkley et al. 7278* (MEXU); Near Tonatico, *Acevedo s.n.* (MEXU). JALISCO: Vicinity of Autlán de Navarro, *Moore & Bunting 8735* (BH, MO); N of La Cuesta, *McVaugh 21262* (MICH); SW of Pihuamo, *McVaugh 24456, 24462* (MICH); S of Puerto Vallarta, *Croat 45427* (MO); Quimixto, *Mexia 1200* (F, GH, MICH, MO, NY, US). MARÍA MADRE ISLANDS: Tres Maria Group, *Maltby 96* (US). MÉXICO: Temascaltepec, *Hinton 3984* (GH, K), *3808* (G, K, NY). MICHOACÁN: S of Arteaga, *Moore & Bunting 8786* (BH, MO), *8792* (BH); Maguile, *Emrick 129* (F). MORELOS: Cuernavaca, *Borgeau 1418* (P), *Matuda 25983* (MEXU, MICH, US), *25933* (MEXU), *Moore & Bunting 8821* (BH); Oaxtepec, *Harking 683* (MEXU), *Matuda 26029* (MEXU, UC). NAYARIT: N of Compostela, *McVaugh 16531* (MICH); Between Tepec and Jalcocotán, *Croat 45243, 45336* (MO); Between Tepic and Jalcocotán, *Moore & Bunting 8708* (BH, MEXU, US); Between Mazatlán and Las Varas, *McVaugh 19025* (MICH). OAXACA: N of Ixhuatán, *King 1997* (US); Betwen Pinotepa and Tlaxiaco, *Croat 45803, 45815* (MO); Between Pochutla and Chacalapa, *Hansen et al. 1543* (MO, WIS); NE of Valle Nacional, *Thurm et al. 229* (UMO); El Vineda, *Conzatti 3463* (MEXU, US). PUEBLA: Vicinity of Xicotepec de Juárez, *Quintero 786* (MEXU). SAN LUIS POTOSÍ: *Rowell et al. 17M350* (F); N of Tamazunchale, *Xolocotzi et al. 7644* (MEXU); NW of Tamazunchale, *Croat 39282A* (MO), *Edwards 581* (F, MO), *Hitchcock & Stanford 6916* (US), *Vines 334* (US). TABASCO: Balancán, Finca La Esperanza, *Calzada et al. 2653* (MO); Vicinity Comalcalco, *West 2716* (WIS); Between Villahermosa and Teapa, *Bravo et al. 110* (MEXU). TAMAULIPAS: S of Ciudad Victoria, *Palmer 309* (F, GH, MO, NY, UC, US), *Meyer & Rogers* (MO). VERACRUZ: *Schnee V-VII* (BH); Biological Station, Laguna Escondida, *Hernández & Vazquez 562* (MEXU); W of Coatzacoalcos, *Croat 32740* (MO); Vicinity of Jalapa, *Baez 127, 560* (F), *Castillo & Tapia 677* (MO), *Hernández 205* (MEXU), *Lot et al. 762* (MEXU), *Ortega 336* (F, MO), *Plunkett 27A* (F); Vicinity Jesus Carranza, *Nevling & Gómez-Pompa 2558* (F); E of Minatitlán, *Barkley & Carr 36219* (GH); NW of Misantla, *Bunting 1658* (US), *Moore & Bunting 8945* (BH, MO), Motzorongo, *Smith 468* (MO); Between Orizaba and Córdoba, *Rosas 405* (A, MEXU, O); Region of Orizaba, *Borgeau 2416* (P); SW of Orizaba, *Croat 39550* (MO); E of Papantla, *Moore & Bunting 8952* (BH); Biological Station at San Andrés Tuxtla, *Calzada 85* (F, Jalapa); Vicinity San Andrés Tuxtla, *Madison 1742, 1743* (GH), *Martínez 2286* (F, Jalapa), *Quintero 710* (MEXU); Between Sarabia and Cerro Quebrado, *Gómez-Pompa & Riba 262* (F); Vicinity of Tantoyuca, *Chiang 10* (MEXU); Vicinity of Tepetzintla, *Chiang 353* (MEXU); NE of Tihuatlán, *Hansen et al. 1766* (MEXU, MICH, MO, WIS); SW of Tlapacoyan, *Nevling & Gómez-Pompa 1125* (MO, Jalapa); SW of Veracruz on Córdoba-Veracruz Road, *Moore & Bunting 8876* (BH).

27a. Syngonium podophyllum Schott, Bot. Zeitung (Berlin) 85:1851. TYPE: Mexico (Schott drawings 3223 and 3226; NYBG Photos 4330 and 4329 respectively).

FIGURES 57–60.—57. *Syngonium mauroanum, Croat 34249*; adult blades (×1/4).—58. *S. mauroanum, Lewis et al. 1637*; adult plant with inflorescences.—59. *S. neglectum, Hiwan 1189*; inflorescence at anthesis (×5/12).—60. *S. neglectum, Hiwan 1189*; inflorescence with cut-out showing pistillate flowers (base) and staminate flowers (above) (×1/2).

Pothos auritus Willd. ex Schult., Mant. 3:301. 1827, non *Syngonium auritum* (L.) Schott. TYPE: Amer. Merid. *Humboldt & Bonpland* (not seen).
Arum auritum Vell. non L., Fl. Flum. 9. *tab. 113*. 1827 (drawing only; no text). TYPE: Brazil (plate only).
Xanthosoma gracile Miq., Delect. Sem. Hort. Amstelodam. 1853. TYPE: Venezuela, Caracas, introduced into horticulture in Amsterdam.
Syngonium vellozianum Schott, Oersterr. Bot. Wochenbl. 4:418. 1854. TYPE: Brazil (Schott drawings 3239 and 3240; NYBG Photos 4318 and 4319 respectively).
S. ruizii Schott, Oesterr. Bot. Wochenbl. 4:148. 1854. TYPE: Peru (Schott drawing, NYBG Photo 4333).
S. gracile (Miq.) Schott, Syn. Aroid. 70.1856.
S. riedelianum Schott, Syn. Aroid. 70. 1856. TYPE: Brazil (based on *Philodendron riedelianum* hort. non Schott, not seen).
S. decipiens Schott, Syn. Aroid. 69. 1856. TYPE: Brazil, Ilheus (based on *Caladium arboreum* hort., Schott drawing 3200; NYBG Photo 4320 of collection of *Erzherzog Maximillian 719*).
S. poeppigii Schott, Syn. Aroid. 68. 1856. TYPE: Peru, Yurimaguas, *Poeppig* (Schott drawing 3226; NYBG Photo 4321) (see discussion).
S. affine Schott, Syn. Aroid. 67. 1856. TYPE: Surinam, Paramaribo, *Wullschlagel 504* (Schott drawing 3192; NYBG Photo 4323).
S. willdenowii Schott, Syn. Aroid. 68. 1856. TYPE: Based on *Pothos auritus* Willd., Herb. No. 3104. fol. 1, *Humboldt* (P?, not seen).
S. xanthophilum Schott, Prodr. Syst. Aroid. 214. 1860. TYPE: Mexico (specimen at W destroyed); photo FM 29870; photo of Schott drawing, NYBG Photo 4335) (see discussion).
S. vellozianum Schott var. *latilobum* Engler, Fl. Bras. 3(2):130. 1878. TYPE: Brazil, Rio de Janeiro, *Riedel*.
S. vellozianum var. *riedelianum* (Schott) Engler, Fl. Bras. 3(2):130. 1878.
S. vellozianum var. *decipiens* (Schott) Engler, Fl. Bras. 3(2):130. 1878.
S. vellozianum var. *poeppigii* (Schott) Engler, Fl. Bras. 3(2):130. 1878.
S. amazonicum Engler, Pflanzenr. IV.23E (Heft 71):128. 1920. TYPE: Brazil, Amazonas, Rio Juruá, *Ule 5614* (B, holotype).
S. podophyllum var. *multisectum* Engler, Pflanzenr. IV.23E (Heft 71):129. 1920. TYPE: Martinique, *Duss 519* (not seen).
S. ternatum Gleason, Bull. Torrey Bot. Club 56:13. 1929. TYPE: Guyana, Waini River, *De La Cruz 1288* (NY, holotype).

Juvenile plant with stems slightly glaucous; petioles sheathed ½–⅔ their length; blades simple, cordate, 7–14 cm long, becoming sagittate or hastate, acuminate at the apex, the anterior lobe somewhat constricted at the base, the posterior lobes usually more or less triangular, directed downward or prominently outward; blades on climbing plants 12–27 cm long. Adult plants with stems sometimes glaucous; sap milky; internodes 2.8–14.5 cm long, 0.5–3.5 cm wide (dry); petioles 15–60 cm long, sometimes glaucous, sheathed ⅔ their length (the sheath free-ending), rounded to obtusely angular above the sheath; blades pedatisect, the surface dark green above, pale below (sometimes glaucescent in South America); leaflets 3–11, united to free; lowermost leaflet variously auriculate at the base, the auricles oblong to oblong-elliptic to broadly elliptic; median leaflet obovate to broadly elliptic, abruptly acuminate at the apex, broadly or narrowly decurrent at the base, 16–38 cm long, 6–17 cm wide; rachis usually angular on blades with more than 3 segments; primary lateral veins 3–4(–7) pairs on the median leaflet, sunken above, prominently raised beneath; collective veins 2 or 3; tertiary veins all distinct. *Inflorescences* 4–11 per axil; peduncle sometimes glaucous somewhat compressed laterally, erect and usually less than 9 cm long at anthesis, pendent, to 13 cm long in fruit; spathe 9–11 cm long; spathe tube sometimes glaucous, narrowly ovoid to ellipsoid, 3–4 cm long, 1.8–2 cm diam., green inside and out; spathe blade greenish white to creamy white or sometimes yellow (in South America) (sometimes green outside and creamy white inside),

6–7.5 cm long, 3–5 cm wide, long-cuspidate at the apex; pistillate portion of the spadix 1–2 cm long, 6–9 mm diam., greenish cream, the flowers irregularly (5–6(–7)-sided, adherent, the stigma discoid-capitate, sometimes 2- or 3-lobed; staminate portion of the spadix 4–7 cm long, 7–15 mm diam., cream, the synandrium with anthers usually 4, cross-shaped, 3.5–4 mm wide, partially or completely fused. *Infructescences* red to reddish orange or yellow (rarely brown) at maturity; syncarp ovoid, brownish, scruffy with darker brown flecks, 3–5.5(–7) cm long, 1.5–3.5 cm wide; seeds many, ovoid, 7–11 mm long, 5–7 mm wide, black or brown, enveloped in a soft, grayish, sweet, pulpy mesocarp. Figs. 64, 65, 69.

DISTRIBUTION: *Syngonium podophyllum* is the most widespread and variable species in the genus, ranging from Mexico (states of San Luis Potosí and Veracruz) to the Guianas, Brazil, and Bolivia. It is found principally on the Atlantic slopes in Mexico but commonly extends to the Pacific slope in Guatemala, Costa Rica, and Panama. It ranges from sea level to usually less than 1000 m and is more abundant below 750 m, especially between 100 and 500 m. *Ellenberg 3857* (Peru, Tingo María-Pucalpa) at 1510 m and *Lehmann 5316* (Colombia, Río Negro in Andes of Popayán) at 1400–1600 m are both well out of the normal range of the species. They are sterile collections and doubtfully placed with *S. podophyllum*. In Central America it is most frequent in regions of tropical moist forest but also occurs in premontane wet forest. It is replaced by *S. macrophyllum* in tropical wet forest life zones.

Syngonium podophyllum and *S. macrophyllum* are often difficult to separate where they occur together in wetter parts of tropical moist forest and in premontane wet forest, but *S. macrophyllum* is usually distinguishable by its much larger vegetative and fertile parts, its smoother, thicker blades, which tend to dry brown rather than greenish as in *S. podophyllum*, and by its ovate-cordate juvenile blades.

The morphological variation in the species is great. Mexican plants may have up to 11 leaflets (usually 9), have leaflets often more widely separated and have stems, peduncles and spathe tubes glaucous, whereas Panamanian populations generally have mostly 3–5 (sometimes 7) leaflets with the lowermost leaflet often conspicuously auriculate.

Unusual variation is also represented in collections from Darién Province, Panama. Here the auricles of the lateral leaflets are frequently obovate and scarcely pinched-off rather than more or less oblong and usually conspicuously pinched-off as is typical of most Central American populations. These Darién populations most closely resemble typical material of what was previously considered *S. vellozianum*.

Infructescences in Mexico are commonly bright red whereas those in Panama and in South America are generally yellow to orange or red orange.

In Central America *S. podophyllum* is most closely related to and confused with *S. angustatum*. The two species occur together in similar habitats throughout much of their range in Central America, and according to Birdsey (1955) they may hybridize. (See the Key for characters used in separating the two species.) *Syngonium podophyllum* may also be confused with *S. neglectum* Schott in its vegetative condition. In the field *S. podophyllum* can be distinguished from *S. neglectum* by its glaucous stems. Although the species tends not to have glaucous

FIGURES 61–64.—61. *Syngonium macrophyllum*, *Croat 25187*; adult plant with young infructescences (×1/8).—62. *S. neglectum* (no voucher); adult plant with young infructescences (×1/10).—63. *S. neglectum*, *Croat 45243*; preadult leaves (×5/12).—64. *S. podophyllum* var. *podophyllum*, *Croat 7027*; adult plant with several stages of preadult leaves (×1/7).

stems in the southern part of its range, there is no confusion with *S. neglectum*, which is restricted to Mexico.

The species is equally variable in South America. I have been unable to separate Central American material from *S. vellozianum* of South America. The widespread *S. vellozianum* was treated by Engler & Krause (1920) as a distinct species based on its having leaflets with the leaf tissue united at the base. However, this is not always the case and the degree of separation of the leaf segments is in fact quite variable, ranging from leaves which have the segments closely united to leaves which have the segments relatively remote from one another. The same is true for the species in Central America, as I have already noted. Other variations in South American material of *S. podophyllum* involve the shape and size of the auricles on the lateral lobes. South American material generally has fewer leaflets (most commonly 3 distinct leaflets with the lateral leaflets conspicuously auriculate) and corresponds to the species in Panama and the lower part of Central America; however, it may have up to 5 distinct leaflets with a prominent "pinched-off" auricle, such as in material Engler and Krause called *S. amazonicum*. All of these characters are extremely variable and are not consistent in material from a single geographical area.

Another synonym of *S. podophyllum* is *S. ternatum*. Type material with this name, like that of *S. yurimaguense*, has poorly developed auricles on the lateral lobes. Considering the immense variability of *S. podophyllum* in a single population (or even on a single plant) there is no justification for maintaining these different leaf forms.

I believe that *S. xanthophilum* is a synonym of *S. podophyllum*. The description was of a sterile collection cultivated in Vienna. The collection as illustrated by Schott's painting (NYBG Photo 4335) represents an apparently juvenile plant. The leaves are remarkably similar to juvenile leaves of *S. podophyllum*. Further evidence that the Schott illustration represents a juvenile of *S. podophyllum* is that a photograph of an adult specimen of *S. podophyllum* was also later made at Vienna. This specimen seen in Field Museum Type Photo 29870 was perhaps collected from the same plant after it was more mature.

Mention should be made of the name *S. auritum* Poeppig which occurs in the literature. Poeppig (1845) prepared a description of *S. auritum* Schott with apparently no intention of considering it a new species. Schott (1856) described *S. poeppigii* saying that it was based on *S. auritum* Poeppig, a nonexistent name. Engler & Krause (1920) in their revision of *Syngonium* included *S. poeppigii* Schott and *S. auritum* Poeppig in synonymy with *S. vellozianum* var. *oblongisectum* Engler thus perpetuating an error by Schott.

Although South American material of *S. podophyllum* may ultimately prove to consist of other subspecies or varieties with additional field work, enough is known at this time to recognize *S. peliocladum* as a variety of *S. podophyllum*. Variety *peliocladum* differs from the typical variety only in having tuberculate projections on the stems. Tom Ray (pers. comm.), who has studied populations in the field in Costa Rica, suspects that these projections may have no taxonomic significance whatever.

Syngonium podophyllum has been collected in flower and fruit throughout the year.

Belize: belize: N of Caves Branch Base Camp, *Whitefoord 1080* (MO); Gracie Rock, *Liesner & Dwyer 1468* (F, GH, MO). cayo: Along Sibun River, *Croat 24866* (MO); Water hole near Vaca, *Gentle 2446* (GH, MICH). toledo: E of San Jose, *Gentry 8133* (MO); Monkey River beyond falls, *Gentle 3943* (GH, MICH).

Bolivia: la paz: Rurrenabaque, *White s.n.* (NY); Puerto Linores, *Beck 1660* (MO); Basin of Río Bopi, *Krukoff 10476* (F, GH, MO, NY). pando: Above Abuña, *Prance et al. 6248* (NY, US).

Brazil: No other location, *Pires & Santos 16463* (NY). acre: Between Mundurucus and Tatajuba, *Maas et al. P12885* (K, NY), *Steward et al. 12885* (US); Between Porangaba and Papagaio, *Maas et al. P13132* (NY, US); NW of Cruzeiro do Sul, *Prance et al. 2813* (NY); Trail to Rio Iaco, *Prance et al. 7738* (NY, US); Vicinity of Campinas, *Forero et al. 6350* (NY, US). amapá: Near mouth of Cricu River, *Egler et al. 47443* (NY, US); At confluence of Rio Oiapoque, *Irwin et al. 48040* (MO, NY, US). amazonas: Vicinity Humaitá, *Krukoff 6074* (GH, K, MO, NY, US), *Prance et al. 3554, 8134* (NY); Juruá, *Ule 5614* (B); Near Palmares, *Krukoff 8055* (F, NY); Near Tabatingo, *Prance et al. 16718* (NY, US). ceará: Serra de Botavite, *Ule 9000* (K). maranhão: Island of São Luís, *Froes 11740* (F). mato grosso: Vicinity of São Loucenço Mines, *Prance et al. 8962* (K, NY, US); Vicinity of Jarú, *Forero & Wrigley 7111* (K, NY, US); Source of Jatuarana River, *Krukoff 1573* (GH, K, NY). pará: *Prance & Silva 58860* (F, GH, K, NY, US); Parque Indigena do Tumucumaque, *Cavalcante 2377* (K, NY, US); Munc. Guaraquecaba, *Hatschbach 18697* (US); Vicinity of Cachoeira, *Prance & Pennington 1798* (NY); Santarém, *Silva & Sousa 2249* (NY, US); Tucuruí, *Silva et al. AS168* (US). pernambuco: Tapera, *Tickel 3349* (US).

Colombia: amazonas: Near Loreto-Yacú River, *Plowman et al. 2408* (F, GH, K), *Schultes & Black 8314* (US). antioquia: Casabe, *Renteria et al. 1940* (MO); Segovia Antioquia, *Renteria et al. 1722* (MO). bolívar: Vicinity Estrella, *Curran 340* (US); Near Turbaco, *Killip & Smith 14660, 14661* (GH, NY, US). boyacá: N of Bogotá, El Umbo, *Lourance 688* (GH). caldas: Aremnia, *Pennell et al. 8660* (GH). cauca: Central Andes of Popayán, *Lehman 5316* (K). chocó: Acandí, *Forero 486* (MO); Hoya del Río San Juan, *Forero et al. 3881* (MO); City of Mutis, *Killip & García 33462* (F, GH, US); Road to Palmar-Novita, *Forero et al. 2413* (MO). meta: E of Puerto López, *Davidse & Llanos 5486* (MO). putumayo: Vicinity of Santa Rosa, *Plowman 2113, Schultes 3615* (GH); Puerto Limón, *Schultes & Cabrera 18713* (US). valle: Buenaventura, *Lehman 5319* (F, K).

Costa Rica: alajuela: Vicinity of Bijagua, *Croat 36324, 36374* (MO); Plains of San Carlos, *Molina et al. 17671* (F, US). cartago: W of Turrialba, *Croat 36828* (MO). guanacaste: S of La Cruz, *Williams & Williams 24528* (F). heredia: Near Río Puerto Viejo, *Burger & Stolze 5859* (F). limón: Jiménez, *Smith 4980* (GH); SE of Limón, *Croat 43172* (MO); S of Punta Cahuita, *Croat 43203* (MO); S of Siguirres, *Croat 43327* (MO). puntarenas: Between Palmar Sur and Piedras Blancas, *Croat 32918* (MO); Osa Peninsula, Rincón, *Burger & Stolze 5569* (F, US), *Burger & Liesner 7302* (F); N of Río Clara, *Croat 32952* (MO).

Ecuador: bolívar: Charquiyacu, *Solis 6129* (F). guayas: Vicinity of Naranjito, *Camp 3584A* (NY). los ríos: Between Mocahi and Palenque, *Dodson et al. 7110* (SEL); Río Palenque Biological Station, *Dodson & Ton 5304* (SEL, US). marona-santiago: Gualaquiza, *Sparre 19038* (S). napo: Between Baeza and Lago Agria, *Croat 49513* (MO); Vicinity of Coca, *Gentry 12526* (MO), *Holm-Nielsen & Jeppesen 831* (C, NY); Limoncocha, *Mowbray 69930* (MO); SE of Tena, *Grubb et al. 1555* (K, NY). pichincha: El Recreo, *Eggers 15131* (C).

El Salvador: ahuachapán: Sierra de Apaneca, *Standley 20157* (F). la libertad: SW of Santa Tecla, *Carlson 154* (UC).

French Guiana: Camopi River, *Oldeman & Sastre 158* (US); Along l'Acarouany River, *Sagot 936* (US).

Guatemala: alta verapaz: Vicinity Cahabón, *Cook & Griggs 679* (US); Finca Sepacuite, *Cook & Griggs 31* (US); Along Río Icbolay, *Steyermark 44748* (F); Latinta, *Smith 1530* (US); Pampajché, *Standley 70586, 70802, 70675* (F); Vicinity Tamahú, *Croat 41492, 41523* (MO); W of Telemán, *Croat 41535* (MO); Vicinity Chiquimula, *Steyermark 30125* (F). izabal: La Libertad, *Lundell 2603* (F), *3523, 3213* (US); S of Puerto Barrios, *Croat 41875* (MO), *LeDoux et al. 2103* (NY); Vicinity Quiriguá Viejo, *Standley 23745* (US), *Steyermark 38472* (F); Río Polochic, *Smith 1532* (GH, K, US); Santo Tomás, *Deam 6049* (GH, MICH, MO, US). petén: Near Cancuén, *Steyermark 45329* (MO), *45537* (F); Santa Elena, *Ortiz 1820* (F, MICH). quezaltenango: Near Patzulín, *Steyermark 33528* (F), *Standley 86881, 86884, 86888, 86903* (F); Near Santa María de Jesús, *Standley 68202* (F). san marcos: Above San Rafael, *Croat 40825, 40843* (MO). sololá: Slopes of Volcán Atitlán, *Steyermark 48017* (F, MO). suchitepéquez: Finca Alotenango, *Standley 65015* (F); SW slopes of Volcán Zunil, *Steyermark 35341* (F).

Guyana: mazaruni-potaro: Mazaruni River, *Fanshawe 4783* (K). northwest: Waini River, Marabo Shortcut, *LaCruz 1288* (NY, US). rupununi: Upper Rupununi River near Dadanawa, *LaCruz 1469* (CM, F, GH, MO, NY, US); NW slopes of Kanoku Mountains, *Smith 3547* (F, GH, K, NY, US).

Honduras: atlántida: Vicinity La Ceiba, *Yuncker et al. 8678* (GH, MO, UC, US); Lancetilla

Valley, *Pffeifer 2069* (US), *Standley 52751, 53330, 54537, 56603, 56648* (F, US), *53486* (US). *Yuncker 5091* (F), *5090* (MICH). COPÁN: Below Copán Antigua, *Barkley & Hernández 40278* (GH); E of Copán, *Croat 42512, 42524, 42527* (MO); Vicinity of ruins of Copán, *Carlson 533* (F, UC). CORTÉS: N of Lago de Yojoa, *Croat 42719* (MO). EL CAYO: Vaca, *Gentle 2599* (MICH). YORO: Quebrada Sica, *Standley 53931* (US). SANTA BÁRBARA: San Pedro Sula, *Thieme 5529* (US).

MEXICO: No other location, *Kenoyer 428* (F). CAMPECHE: Santa Leonor, *Barlow 14-3* (MICH, WIS). CHIAPAS: Between Chiapilla and San Lucas, *Laughlin 278* (F, MEXU); Escuintla, *Matuda 16723* (GH), *s.n.* (7-12-47, 8-30-47) (MEXU), *17939, 20946* (MEXU); S of Isthuatán, *Croat 47835* (CAS, MEXU, MO); N of Isthuatán, *Croat 47870* (MO); SE of Mapastepec, *Breedlove & Thorne 30680* (MO); Munc. of Las Margaritas, on Guatemala Border, *Breedlove & McClintock 34088* (DS); Ocosingo, *Breedlove 33950, 34463* (DS); N of Ocozocoautla, *Breedlove 38214* (DS), *Croat 40629, 40652* (MO); SW of Palenque, *Croat 40318, 40338* (MO); N of Pichucalco, *Croat 40083* (MO); NW of Pueblo Nuevo Solistahuacán, *Croat 47799* (MO); WNW of Soyalo, *Breedlove 37216* (DS); Between Tapachula and Unión Juárez, *Croat 47204* (MO). GUERRERO: Acapulco and vicinity, *Palmar 346* (F, GH, MEXU, MO, UC, US); E of Agua de Obispo, *Crisman & Willis* 292 (MICH); NAYARIT: NW of Jalcacatlán, *Croat 45306* (MO). OAXACA: Cahuapa River, *Williams 8905* (F); Island of Malsaya, *Quintero 657* (MEXU); Near Junction of Ismo Highway and Road to Matías Romero, *Carlson 2193a* (F, MO); Tuxtepec, *Chavelas & Perry 237* (MEXU); *Chavelas 278* (MEXU); *Martínez & Calderón 556* (GH, MEXU, UC, US); Ubrero, *Williams 9290, 9525* (F); S of Valle Nacional, *Croat 39721, 39737* (MO); NE of Valle Nacional, *Moore & Bunting 8909* (BH). PUEBLA: No other location, *Bravo 520* (MEXU); Near María Andrea, *Rzedowski 23379* (MICH). SAN LUIS POTOSÍ: *Palmer s.n.* (US); NW of Huichihuayán, *Croat 39247* (MO); NW of Tamazunchale, *Croat 39282* (MO), *Dunn & Dunn 19152* (MO); Xilitla, *Villar & Hernández 7145* (MEXU). TABASCO: W of Cárdenas, *Conrad et al. 2767* (MO); Road to del Golfo, *Contu 176B* (MEXU); Between Macuspana and El Carmen, *Gilly & Hernández 367* (MICH); Near Teapa, *Matuda 37496* (MEXU). TAMAULIPAS: NNW of Gómez Farías, *Martin 69* (MICH). VERACRUZ: *Lot 637* (Jalapa); Near Boca del Río, *Paxson et al. 17M634* (F, MEXU); Campo Experimental de Hule, El Palmar Zongolica, *Santos 2317, 3634* (MICH); Caña de las Perdidas, *Chavelas et al. 2372* (MEXU); W of Catemaco, *Quintero 1495* (MEXU); Cerro Gordo, *Dorantes et al. 4261* (Jalapa); E of Coatzacoalcos, *Croat 40061* (MO); Coatzacoalcos River, *Williams 8420* (MICH); Between Conejo and Huatusco, *Moore & Bunting 8865* (BH, MO); Along Highway 185, N of border of Veracruz, *Croat 40010* (MO); Hidalgotitlán, *Vázquez 782* (F, Jalapa, MEXU); S of Highway between Córdoba and Veracruz, *Croat 39616* (MO); S side of Laguna de Sontecomapau, *Lot 1285* (F, GH, MEXU); Lake Catemaco, *Calzada 54* (F); Road to La Palma and Balzapote, *Calzada 2447* (F, Jalapa, MO); Las Choapas, *Soto & Horowitz 49* (Jalapa); N of Martínez de la Torre, *Nevling & Gómez-Pompa, 532* (GH, MEXU); NE of Minatitlán, *King 1042* (MICH); District of Papantla, *Kelly 156, 269* (BH); Between Papantla and Tajín, *Moore & Bunting 8955* (BH); Road to Playa Escondida, *Breckon & Breckon 2043* (MO); Rancho Tepellaw, *Hernández s.n.* (Jalapa); San Andrés Tuxtla, *Dressler & Jones 25* (GH), *Kennedy & Horvitz 3687* (F), *Soto & Horvitz 30* (F), *Sousa 2107* (MEXU); San Francisco, *Smith 1307* (F); E of San Pablo, *Gutiérrez 9* (MEXU); Vicinity Santiago Tuxtla, *Leija & Garza 5418* (MEXU); On Road to Santecomapan, *Moore & Bunting 8934* (BH); W of Sayula de Alemán, *Croat 40023* (MO); S of Tampico, *Palmer 386* (GH, MO, US); YUCATÁN: Chichen Itza, *Lundell & Lundell 7506* (MEXU, MICH).

NICARAGUA: CHONTALES: Above Cuapa, *Stevens 3694* (MO). JINOTEGA: SE of Yali, *Croat 42934* (MO). ZELAYA: Alamicamba above Río Prinzapolca, *Neill 3901* (MO); E of Siuna, *Neill 4511* (MO).

PANAMA: BOCAS DEL TORO: Chiriquicito, *Lewis et al. 2049* (GH, MO); Vicinity of Chiriquí Lagoon, *Von Wedel 2616* (GH); Station Milla 7.5, *Croat 38128* (MO). CANAL ZONE: Barro Colorado Island, *Aviles 35* (F), *Croat 5815, 7027, 7429, 8913, 10197, 11694, 16218, 20888* (MO), *10260, 11426, 11921* (F, MO), *10876* (F, MO, PMA, UC), *12558* (F, MO, SCZ), *Foster 1939* (F, GH, MICH, PMA), *Gentry 428* (MO), *Hutchison & Wright 2864* (UC), *Shattuck 54* (F, GH, MO), *Standley 40914* (US), *Woodworth & Vestal 585* (F, GH, MO); SE of Achiote, *Gentry & Nee 8663* (MO); Near Alhajuela, *Dodge 16596* (MO); N of Frijoles, *Standley 27451* (US); Vicinity Gamboa, *Croat 32975* (MO), *32977* (PMA), *Nee 7745* (US), *Standley 28419* (US); Quebrada Bonita, *Steyermark & Allen 17211* (MO); S of Río Providencia, *Tyson & Blum 4003* (MO, SCZ); Near Summit Gardens, *Dodge & Hunter 8661* (MO). CHIRIQUÍ: Burica Peninsula, vicinity of Puerto Armuelles, *Busey 466* (MO, NY), *Croat 21936, 26704, 35055* (MO), *Liesner 67* (F, MO), *504* (MO, US), *Woodson & Schery 930* (F, NY); Vicinity of Gualaca, *Croat 49822* (MO); Vicinity of Palmas Bellas, *Mori & Kallunki 1971* (MO). COLÓN: SW of Portobelo, *Liesner 1080* (US); E of Portobelo, *Liesner 1109* (MO, US); Vicinity of Portobelo and Nombre de Dios, *Croat 33553, 33636, 49784* (MO); Vicinity Portobelo, *Croat 49746* (MO). DARIÉN: Vicinity of gold mine at Caná, *Croat 37599, 37659, 37676, 38034* (MO); Cerro Sapo, *Hammel 1257* (MO); Vicinity El Real, *Duke 5013* (MO, GH), *Gentry & Clewell 6917* (MO), *Pittier 6568* (GH, US); Vicinity of Paya, *Stern et al. 199* (GH, MO, US); Río Tuquesa, *Le Clezio 188* (MO), PANAMÁ: Vicinity of Cerro Azul, *Croat 11508* (MO); El Llano-Cartí Road, *Croat 33776* (MO), *Nee 10520* (US); Vicinity Río Majé, *Croat 14524, 34438, 34658* (MO).

PERU: AMAZONAS: Río Cenepa, *Ancuash 122, 1157, 1193* (MO), *Berlin 371* (MO); S of Chávez Valdivia, *Berlin 838* (MO). AYACUCHO: Near Kimpitirique, *Killip & Smith 23007* (NY, US). HUÁNUCO: Honoria, *Schunke 1592* (F); Tingo María, *Ellenberg 3826, 3857* (MO). JUNÍN: N of La Merced, *Killip & Smith 23626* (NY, US). LORETO: Iquitos, *Killip & Smith 27398, 27448* (NY, US), *Martin et al. 1636* (F); La Victoria, *Williams 2631* (F), *2782* (F, US); Leticia, *Williams 3054* (F); Province Maynas, *Diaz & Jaramillo 9* (MO), *Revilla 1087* (MO); N of Iquitos, *Revilla 855* (MO); Río Huallaga, *Williams 4986* (F, US), *Croat 17855* (MO); Soledad on Río Itaya, *Killip & Smith 29680* (NY, US); NE of Yurimaguas, *Killip & Smith 27901* (US). MADRE DE DIOS: Parque Nacional de Manú, *Foster & Janson 5216* (F), *Gentry et al. 26771* (MO), *Terborgh 6624* (F); Tambopata, *Gentry & Revilla 16299* (F, MO, NY). SAN MARTIN: Mariscal Cáceres, *Gentry et al. 26733* (MO), *Schunke 3862 4932* (F, GH, MO, NY, US), *7711* (MO, US).

PUERTO RICO: At Km 28.1 on Route 191 near Florida, *Wagner 1003* (MICH).

SINGAPORE: No other location, *Clemens 22553* (UC).

SURINAM: No other location, *Samuels 175* (GH, K); Corantijn River, *Boer & Wessels 548* (A); Slopes of Hendriktop, *Daniels 978* (US); Jodensavanne-Mapane creek area, *Lindeman 4782* (F, MO, NY); Lucie River, *Maguire et al. 53991* (NY), *Prance et al. 54619* (F, K, NY, US), *Prance et al. 55668* (NY); N of Paramaribo, *Maguire & Stahel 22800* (F, NY, US); Tibiti, *Lanjouw & Lindeman 1616* (K, NY, US).

TRINIDAD: Siparia Quarry, *Britton & Broadway 2795* (NY, US).

UNITED STATES: FLORIDA: Coral Gables, *Kaplan 478* (UC); Madiera Beach, *Anderson & Mason 19328* (CM).

VENEZUELA: AMAZONAS: Tencua, *Colchester 2052* (K); Vicinity Mision de Santa María de los Guaicas, *Steyermark 106164* (MO, VEN). APURE: San Camilo Forest Reserve, *Steyermark et al. 101396* (MO, NY, VEN). BARINAS: Vicinity of Barinas, *Bunting 2271* (MY); SW of Barinas, *Smith 3292* (MY, VEN); Caño Barragán, *Bunting 2257* (MY); Caparo Forest Reserve, *Steyermark et al. 102051* (MO, VEN); Río Caparo, *Liesner & González 9413* (MO). BOLÍVAR: S of Plateau of Nuria, *Bunting & Holmquist 4317* (MY); Vicinity of Salto Pará, Río Caura, *Steyermark et al. 113104* (F, MO, US). DELTA AMACURO: Sierra Imataca, *Steyermark 87381* (F, K); Tucupita, *Davidse & González 16548* (MO). MÉRIDA: Between San Cristóbal and El Vigía, *Bunting 2403* (MY). TÁCHIRA: Vicinity of San Cristóbal, *Broadway 578* (US). Vicinity La Grita, *Bunting 2483, 2491, 2497, 2500* (MY); E of Hacienda El Palmar, *Steyermark et al. 120463* (MO). TRUJILLO: La Ceiba, *Williams 12661* (US). ZULIA: S of Concha, *Bunting 2774, 2788* (MY); Hacienda Las Chorros, *Farrari & Trujillo 1569* (MY); Sierra de Perijá, *Steyermark & Fernández 99633A* (NY, US); SE of Mission of Los Angeles de Tocucu, *Steyermark 99878* (US).

27b. Syngonium podophyllum Schott var. **peliocladum** (Schott) Croat, comb. nov.

S. peliocladum Schott, Prodr. Syst. Aroid. 202. 1860. TYPE: Costa Rica, *Wendland* (type destroyed, Schott drawings 3215, 3216; NYBG Photos 4327, 4328).

Juvenile plants with stems not glaucous, usually dark violet purple; petioles sheathed from ½ to nearly the entire length; blades hastate to sagittate, the anterior lobe ovate, acuminate, the posterior lobes ovate to lanceolate, acute at the apex. Adult plants with stems not glaucous; internodes 0.4–1.5 cm diam., 1–20 cm long, usually densely covered with brownish projections; petioles 11–33 cm long, usually sheathed $^1/_2$–$^4/_5$ or more of their length, obtusely 1-ribbed adaxially; blades trisect to almost 5-lobed, mostly 16–33 cm long, often drying yellowish green; lateral leaflets free or confluent, usually conspicuously auriculate and usually nearly pinched-off to form a small lobe, the auricle directed at right angles to the axis of the lateral leaflets; median leaflet 14–25 cm long, ovate to elliptic, acuminate at the apex, acute to cuneate at the base; primary lateral veins 3–8 pairs, sunken above, raised beneath; collective veins 2 or 3; tertiary veins all clearly visible. *Inflorescences* usually 6–8 per axil; peduncles not glaucous, 3.5–11 cm long and erect at anthesis, 7–14 cm long and pendent in fruit; spathe tube ovoid to ellipsoid, usually not glaucous, 2–3 cm long, green inside and out; spathe blade greenish white to cream, 4–5.5 cm long, pistillate portion of the spadix 1–2 cm long; staminate portion of the spadix 4–6 cm long, the flowers similar to

those of *S. podophyllum*. *Infructescences* yellow to orange, 4–5 cm long, 3–3.5 cm diam. Figs. 66, 70.

DISTRIBUTION: *Syngonium podophyllum* var. *peliocladum* is known from Costa Rica and Panama, principally on the Atlantic slope from sea level to ca. 1000 m. In Panama it occurs only in Bocas del Toro Province. It occurs in tropical wet forest, premontane wet forest and wetter parts of tropical moist forest.

This variety is recognized by its trisect to almost 5-lobed leaves, usually several inflorescences, and stems which bear conspicuous tuberculate excrescences. Though previously considered distinct from *S. podophyllum*, it is distinguished from that species only by the stem excrescences, and the two taxa overlap in most of the characters previously used to separate them.

Flowering inflorescences are known from June through December. Immature fruits are found more or less throughout the year.

COSTA RICA: CARTAGO: Vicinity Chitaría, *Solis 241* (F); Las Vueltas, Tucurrique, *Tonduz 12891* (US). HEREDIA: Finca La Selva, *Croat 44306* (MO); Near Puerto Viejo, *Croat 35677* (MO). LIMÓN: N of Bribri, *Burger & Antonio 10943* (F); Vicinity of Cairo, *Standley & Valerio s.n.* (US); La Colombiana Farm, *Standley 36975* (US); Vicinity Llanuras de Santa Clara, *Smith 4980* (US); Between Siguirres and Río Pacuare, *Burger & Liesner 6931* (MO).

PANAMA: BOCAS DEL TORO: Above Almirante, *Gentry 2745* (MO); W of Almirante, *Croat 38225* (MO); Vicinity Changuinola, *Croat 38082* (F, MO), *Lewis et al. 954* (GH, K, MO, UC, US); Chiriquicito, *Lewis et al. 2022* (MO); Vicinity of Chiriquí Lagoon, *von Wedel 1025, 2616, 2765* (F, GH, MO); Between Quebrada Treglo and Puerto Palenque, *Kirkbride & Duke 533* (MO); Río Cricamola, between Finca St. Louis and Konkintoi, *Woodson et al. 1915* (MO); Station Milla 7.5, *Croat & Porter 16305* (MO), *Croat 38088, 38115* (MO); Water Valley, *von Wedel 1545* (MO).

28. Syngonium salvadorense Schott, Oesterr. Bot. Z. 8:178. 1858. TYPE: El Salvador, Santa Anna, *Wendland s.n.* (P?, not seen; drawing of type by Schott 3231, NYBG Negative 4331 seen).

S. donnell-smithii Engler, Bot. Jahrb. Syst. 37:141. 1905. LECTOTYPE: Guatemala, Escuintla, Escuintla, 1100 ft, *Donnell Smith 2782* (B, lectotype; M, isolectotype)

Juvenile plants with stems glaucous; internodes 5–20 cm long, less than 1 cm thick; petioles 12–25 cm long, glaucous, sheathed beyond the middle (sometimes more than $^4/_5$ their length); blades usually hastate, sometimes sagittate, 9–19 cm long, 5.5–11 cm wide, the anterior lobe equilateral or inequilateral, often constricted at the base, the posterior lobes inequilateral, usually longer than broad; intermediate blades becoming larger, more conspicuously hastate-lobed, mostly 20–30 cm long, the lobes ovate to broadly ovate, directed markedly outward, eventually becoming pinched off. Adult plants with stems glaucous, frequently scandent; internodes 3–14 cm long, 1–2 cm diam., olive green when young, the periderm tan, thin and cracking; petioles slightly paler than the stems, 18–42 cm long, sheathed $^1/_2$–$^4/_5$ their length, obtusely ribbed above the sheath, the sheath free-ending and acute at the apex; blades trisect to sub-5-sect, the lobes usually confluent to almost free, the median lobe broadly ovate to ovate-elliptic, 14–28 cm long, 8–18 cm wide, acuminate at the apex, rounded at the base, the lateral lobes ovate, unequal, usually not auriculate, sometimes with hastate auricles, rarely the auricles nearly pinching off to form a nearly 5-lobed blade; primary lateral veins 2–5 pairs, mostly arising in the lower half of the blade, slightly sunken on the upper surface, raised beneath; tertiary veins clearly visible on the

FIGURES 65–68.—65. *Syngonium podophyllum* var. *podophyllum*, *Croat 45306*; adult plant with inflorescences at anthesis, unopened (×3/10).—66. *S. podophyllum* var. *peliocladum*, *Croat 38082*; adult plant with inflorescence at anthesis (×1/5).—67. *S. salvadorense*, *Croat 43867*; adult plant with juvenile infructescences (×1/8).—68. *S. triphyllum*, *Croat 35111*; adult plant with young infructescences (×1/10).

lower surface. *Inflorescences* 1 or 2 per axil; peduncles 9–18 cm long and more or less erect in flower, 9–25 cm long and pendent in fruit; spathe tube ellipsoid, 4–5 cm long, 3–4 cm diam., green outside, the inside reddish at the base, greenish near the apex; spathe blade broadly ovate, 7–10 cm long, 4–5 cm wide, greenish outside, the inside white, abruptly cuspidate at the apex; pistillate portion of the spadix 1.5–2.5 cm long, 1–1.5 cm diam., greenish, the flowers with stigmas bilabiate; the staminate portion of the spadix white, clavate, 5–7 cm long, 1–1.5 cm diam., the synandrium irregularly 6-sided, flat at the apex with no sign of fusion, the margins weakly scalloped. *Infructescences* red orange to red, often massive, 9–12 cm long, 6–8 cm diam.; syncarp brown, to 8 cm long and 5 cm diam.; mesocarp sweet, fleshy, white; seeds black, ovoid-ellipsoid, 8–12 mm long, 4–6 mm diam. Fig. 67.

DISTRIBUTION: *Syngonium salvadorense* ranges from southwestern Mexico (Chiapas) along the western coast of Guatemala to El Salvador. It occurs principally in tropical moist forest from sea level to 700 m.

The species is not confused with any other but resembles *S. neglectum* in having large and often solitary inflorescences.

The species is a conspicuous plant in disturbed areas and often grows in great profusion, to the exclusion of most other epiphytic plant species, on the shade trees in coffee plantations in Guatemala.

Flowering inflorescences have been found in February and August. Fruits are mature mostly in July and August.

EL SALVADOR: AHUACHAPÁN: NE of San Francisco Menéndez, *Croat 42074* (MO), *Padella 324* (US). SAN SALVADOR: No other location, *Calderón 924* (US); Vicinity of San Salvador, *Renson 268* (NY, US); Tonacatepeque, *Calderón 2273* (GH, US). SONSONATE: Vicinity of Sonsonate, *Standley 22320, 22337* (GH, NY, US). SAN VINCENTE: Vicinity of San Vincente, *Standley & Padella 3745, 3746, 3798* (F).

GUATEMALA: ESCUINTLA: No other location, *Smith 2782, 2783, 2238* (B, NY, US); Escuintla, *Standley 89211, 89311* (F); Finca Cuyuta, *Smith 2235, 2238* (US); San José, *Standley 64081, 64200* (F); Santa Lucía Cotzumalguapa, *Kellerman 5266* (MEXU, US), *Standley 63442* (F). RETALHULUE: Finca Las Delicias near Retalhulue, *Standley 88044* (F); Vicinity of Retalhulue, *Standley 66788, 87259, 87294, 87400, 88278* (F); San Felipe, *Smith 2781* (US); SANTA ROSA: Cuilapa, *Standley 77982* (F); Near Guazacapán, *Standley 78640, 78965, 78974, 79038, 79055* (F); N of Las Cerritos, *Standley 79562, 79579a* (F). SUCHITEPÉQUEZ: Vicinity of Mazatenango, *Croat 43758* (MO), *Standley 88865* (F), *White 5184* (F, MICH); Vicinity of Tiquisate, *Steyermark 47707* (F, US).

MEXICO: CHIAPAS: Vicinity of Escuintla, *Croat 43867, 47533* (MO), *Matuda 16512* (F, MEXU, MICH, NY), *17695, 17881* (DS, F, MEXU, NY), *17792* (DS, MEXU), *17858, 17937, 17970* (MEXU), *18715* (MEXU, US), *37675* (DS); Vicinity of Finca Prusia, *Breedlove 38652* (DS); NW of Huixtla, *Breedlove & Smith 22534* (DS); NE of Huixtla, *Breedlove 30921* (DS); Pueblo Nuevo Solistahuacán, *Matuda 17831* (MEXU); SE of Tonalá, *Breedlove 25638* (DS); Vicinity of Tuxtla Gutiérrez, *Breedlove 37771* (DS).

29. Syngonium sparreorum Croat, sp. nov. TYPE: Ecuador, Cotopaxi, Río Guapara, ca. 20 km NW of El Corazón, monsoon forest, ca. 250 m, *Sparre 17193* (S, holotype).

Caudex 1–1.5 cm diam.; lamina trisecta aut 5-pedatisecta; petiolus 29–47 cm longus, ad ½–⅔ longitudinalis usque anguste vaginatus; lamina elliptica ad obovata-elliptica, segmentum medium equalis, segmenta lateralia inaequalia leviter, venis lateralibus utroque latere 10–12, fere rectangularibus. Inflorescentiae 2; pedunculus 7–10 cm longus, gracilis; spathae tubus 5–6 cm longus, oblongus-ovoideus, 1.5–2 cm diam.; spathae lamina 7.5–8.5 cm longa, ovata, apice cuspidate; spadix parte feminea 10–12 mm longa, parte mascula spadicis 6–7.5 cm longa; infructescentia pendula, spathae tubo atropurpureo; spadix ad 9.5 cm longa; semina atera, ca. 7 mm longa.

Hemiepiphytic vine; stem 1–1.5 cm diam., drying pale brown; internodes elongate, 6–7 cm long near the apex; petioles 29–47 cm long, narrowly sheathed ½–⅔ their length, to 7.5–10 cm from the apex, the apex of the sheath slightly free from the petiole; blades trisect to 5-pedatisect, the leaflets distinctly free; median leaflet equilateral, elliptic to obovate-elliptic, abruptly acuminate at the apex, cuneate to acute at the base, 17–28 cm long, 9.5–12 cm wide, the leaf tissue decurrent to near the base, the lateral leaflets slightly inequilateral, obtuse to acuminate at the apex, 14–25 cm long, 5.3–9 cm wide, the base narrowly acute on the inner side, obtuse to rounded or conspicuously auriculate on the outer side, the auricles conspicuously constricted at their base; petiolules 7–17 mm long, sometimes free; outermost leaflets nearly oblong to ovate-oblong, 8–10 cm long, 2.7–7 cm wide, narrowly rounded to acute at the apex, the blade surfaces drying yellowish brown; primary lateral veins mostly 10–12 pairs, mostly joining the midrib at a nearly 90° angle, curved to the collective vein; collective vein 3–10 mm from the margin, almost straight or conspicuously loop-connecting with the primary lateral veins; reticulate veins very fine and close but clearly visible on dried material. *Inflorescences* 2 in uppermost leaf axil, erect; prophylls ca. 15 cm long, obtuse at the apex, apparently caducous; peduncles 7–10 cm long, slender, 2–4 mm diam. (dried); spathe tube 5–6 cm long, oblong-ovoid, 1.5–2 cm diam.; spathe blade 7.5–8.5 cm long, ovate when open, cuspidate at the apex, thinly coriaceous, drying brown, soon caducous; pistillate portion of the spadix 10–12 mm long, 5 mm diam. (dried), the flowers ca. 1.5 mm diam., in 5 or 6 spirals, the stigmas raised, ca. 1 mm diam.; staminate portion of the spadix 6–7.5 cm long, clavate, ca. 1 cm diam. in the widest part, conspicuously constricted just above the sterile staminate flowers, the fertile staminate flowers ca. 3 mm long, rounded to irregularly 4–6-sided, the apex of the synandrium truncate, entire, the margins minutely crenulate; sterile staminate portion of the spadix ca. 14 mm long, ca. 8 mm diam. the sterile staminate flowers ca. 2.5 mm long, 1.5–3 mm diam., mostly free from one another, rarely fused. *Infructescences* pendent; peduncle to 13 cm long, to 7 mm diam.; spathe tube oblong-ellipsoid, gradually tapered to both ends, to 13 cm long and 5 cm diam., apparently dark violet purple; fruiting spadix oblong-ovoid, to 9.5 cm long on the front side, 6.5 cm long on the back side, ca. 4.5 cm diam.; seeds black, oblong-ovoid ca. 7 mm long. Figs. 71, 72.

DISTRIBUTION: The species is known only from the type locality on the Pacific slope of northcentral Ecuador.

It is named in honor of the co-author of the *Flora of Ecuador*, Baron Benkt Sparre, who has made the only collections of the species. *Syngonium sparreorum* is probably closest to *S. gentryanum* from Huánuco Department, Peru, but differs in being 5-pedatisect in part and in having the primary lateral veins of the leaflets more numerous and joining the midrib at a nearly 90° angle.

Flowers and immature fruits were found in June.

ECUADOR: COTOPAXI: Río Guapara NW of El Corazón, 250 m, *Sparre 17096, 17101, 17193, 17212, 17297* (S).

30. Syngonium standleyanum Bunting, Baileya 14:21. 1966. TYPE: Costa Rica, Guanacaste, El Arenal, 485–800 m, *Standley & Valerio 45248* (US-1254001, holotype).

FIGURES 69–72.—69. *Syngonium podophyllum* var. *podophyllum*, *Croat 45306*; adult leaves (×⅛).—70. *S. podophyllum* var. *peliocladum*, *Croat 38082*; adult stem showing projections and open inflorescence (×2/5).—71. *S. sparreorum*, *Sparre 17297*; adult blade and inflorescences.—72. *S. sparreorum*, *Sparre 17193*; adult blade and infructescences.

Juvenile plants with scandent stems, not glaucous; internodes 2.3–6.5 cm long; petioles sheathed more than $^4/_5$ their length, 4–12 cm long; blades elliptic, inequilaterally acuminate at the apex, 4–10 cm long, 2–4 cm wide; intermediate leaves elliptic to oblong or lanceolate, subhastate or cordate at the base. Adult plants with stems green, not glaucous, densely and minutely papillate, drying pale brown with longitudinal wrinkles; internodes 3–12 cm long, less than 1 cm diam.; petioles 25–35 cm long, sheathed $^2/_3$ or nearly the full length (1.5–9 cm from the apex), the portion above the sheath acutely angled on the upper side; blades trisect, the leaflets free; median leaflet slightly to very inequilateral, elliptic to oblong, 18–28 cm long, 6.5–12 cm wide, acuminate and mucronate at the apex, acute and attenuate at the base; lateral leaflets elliptic-oblong, 11–24 cm long, slightly if at all more inequilateral than the median leaflet, acute-cuneate on the inner edge at the base, obtuse to rounded or slightly auricled on the outer edge at the base; petiolule 5–15 mm long; primary lateral veins ca. 6 pairs, sunken above, raised beneath; smaller veins clearly visible (at least on drying). *Inflorescences* solitary; peduncle 4.5–5.2 cm long, less than 4 cm diam. on drying; spathe 11.5 cm long; spathe tube green, 4.5–5 cm long, ca. 3 cm diam., fusiform-cylindroid; spathe blade white, ovate-elliptic, 6.2–7 cm long, ca. 2.5 cm diam. (closed), ca. 3.5 cm wide (open), acuminate at the apex, 2.8 cm longer than the spadix; spadix 8.1 cm long; staminate portion of the spadix clavate, creamy white, ca. 6 cm long. *Infructescences* unknown.

DISTRIBUTION: *Syngonium standleyanum* ranges from Honduras to Costa Rica on the Caribbean slope. In Costa Rica it occurs in tropical wet forest and premontane wet forest at elevations from near sea level to about 500 m.

Bunting (1966) reported that the species could be distinguished by the matte upper blade surfaces, deeply impressed primary lateral veins, and the shape of the leaf blade. In addition the densely papillate stem is characteristic. The species is perhaps closest to *S. mauroanum* but that species lacks the densely papillate stems, usually has more prominently hastate posterior lobes, and occurs in tropical moist or premontane moist forest.

Birdsey (1955) proposed a new species to be called *S. stenophyllum* but the name was never published. It was to have been based on *Donnell-Smith 6807* (US-936784) and *Birdsey 335* (UC, US). I have seen the former and it is *S. standleyanum*.

COSTA RICA: GUANACASTE: El Arenal, *Standley & Valerio 45248* (US); Vicinity of Tilarán, *Standley & Valerio 44313* (US). LIMÓN: La Concepción, *Smith 6807* (US). PUNTARENAS: Osa Peninsula, Parque Corcovado, *Ray 3, 17, 18, 19, 44* (GH).

HONDURAS: ZELAYA: In forest behind Bluefields, *Bunting & Licht 1250* (K, US).

31. **Syngonium triphyllum** Birdsey ex Croat, sp. nov. TYPE: Costa Rica, Heredia, near Puerto Viejo along the Río Sucio, 20 m, *Croat 35675* (MO-2381577, holotype).

Caudex 1–2.5 cm diam.; lamina plerumque trisecta, saepe basi auricula conspicua spathulata; petiolus 11–50 cm longus, ad $^2/_3$–$^4/_5$ longitudinalis usque vaginatus, apice acute triangulari; lamina media ovata ad oblonga-elliptica aut elliptica, aequilatera, 17–32 cm longa, lamina lateralis ovata-elliptica ad elliptica, fere aequilatera aut inaequilaterissima et basi auriculata, venis conspicue depressis. Inflorescentiae 1–3(–5); pedunculus 5–7 cm longus; spathae tubus anguste ellipsoideus, 4.5–

6 cm longus, 2–2.5 cm diam., intra viridis pallide, extra rubus; spathae lamina oblonga-elliptica ad oblonga, albida, 8–9 cm longa, cucullata; spadix parte feminea 1.9–2.5 cm longa, stigmate sessili, cupulato.

Juvenile plants at first with short internodes (5 mm or less), becoming scandent, not glaucous, green to greenish brown, turning brown with age; internodes to 17 cm long; petioles sheathed $^{4}/_{5}$ or nearly their entire length, less than 10 cm long, the sheath with the margin crisped; blades inequilateral, elliptic, acuminate at the apex, acute to obtuse and often inequilateral at the base, sometimes weakly cordate, 6–23 cm long; 3–9 cm wide. Intermediate plants with petioles 14–28 cm long; blades entire and elliptic to oblong-elliptic or ovate-elliptic or becoming auricle-lobed at the base, the auricles held parallel to the petiole, in later stages becoming more trisect, the lobes oblong-elliptic, directed at nearly right angles to the midrib. Adult plants with stems not glaucous, sometimes branched; internodes to 9 cm long, to 2.5–3.5 cm long on flowering portions, 1–2.5 cm diam., brown, matte, sometimes drying flaky, sometimes with sharp longitudinal wrinkles; petioles 11–50 cm long, sheathed $^{2}/_{3}$–$^{4}/_{5}$ their length or more, the unsheathed portion sharply triangular with the lateral margins sharply raised; blades usually trisect but frequently with a conspicuous spatulate auricle at the base, the auricle sometimes to 15 cm long, the blade thus appearing almost 5-pedatisect; leaflets free, semiglossy above, dark green, drying dark, the lower surface slightly paler; median leaflet ovate to elliptic or oblong-elliptic, equilateral or nearly so, 17–32 cm long, 6–14 cm wide, short-acuminate at the apex, cuneate or obtuse at the base; lateral leaflets of well-developed blades 15–28 cm long, 4–11 cm wide, ovate-elliptic to elliptic, nearly equilateral to very inequilateral and variously auriculate at the base, the auricles oblong to spatulate to oblong-elliptic, 6–16 cm long; primary lateral veins 10–16 pairs, scarcely more prominent than the interprimary veins, the latter numerous, the primary, major secondary veins and collective veins prominently sunken, prominently raised on the lower surface, the smaller veins clearly visible when fresh; reticulate veins often very close and fine on drying, the collective veins 3–12 cm from the margin, moderately straight or broadly arching between the primary lateral veins. *Inflorescences* 1–5 per axil, usually 1–3, most frequently 1 or 2; peduncles erect, 5–7 cm long in flower, 8–13 cm long and pendent in fruit; spathe ca. 14 cm at anthesis; spathe tube narrowly ellipsoid, 4.5–6 cm long, 2–2.5 cm diam., pale green outside, red inside to near the apex; spathe blade oblong-elliptic to oblong, white on both sides, short cuspidate and weakly cucullate at the apex, 8–9 cm long, ca. 3.5 cm diam. (to 5 cm wide when flattened); pistillate portion of the spadix 1.9–2.5 cm long (fresh) (1–1.8 cm long dry), 7–13 mm diam., pale yellowish white, the flowers irregularly 4-sided, the stigma sessile, cup shaped; staminate portion of the spadix 6–10 cm long, 1–1.5 cm diam., clavate, gradually attenuate toward the sterile flowers, the fertile staminate flowers 4-staminate, the anthers partially or completely fused, the synandrium truncate or slightly rounded at the apex, the staminate sterile flowers slightly longer than the adjacent fertile staminate flowers and much longer than the pistillate flowers, 4–6-sided to ellipsoid or subglobose; the spathe tube becomes rolled backward along its lateral margins and the fleshy white spadix is prominently displayed against the bright red interior of the spathe tube. *Infructescences* oblong-elliptic, green tinged with purple, becoming violet purple on the

FIGURES 73–76.—73. *Syngonium triphyllum*, *Croat 35675*; adult plant with young infructescence (×1/5).—74. *S. triphyllum*, *Croat 36484*; immature infructescences (×1/2).—75. *S. triphyllum*, *Croat 36484*; mature infructescence showing method of display of fruit (inner surface of spathe red) (×2/5).—76. *S. wendlandii*; adult plant with inflorescence at anthesis (Photo by J. Bogner) (×1/4).

outside, the inner surface bright red; spadix oblong-ellipsoid, 6–8 cm long, 3.5–4 cm diam.; mesocarp white, fleshy, sweet; seeds black, irregularly ovoid to ellipsoid, 5–8 cm long, 4–6 cm wide. Figs. 68, 73–75.

DISTRIBUTION: *Syngonium triphyllum* ranges from the northern Atlantic coast of Honduras to central Panama. It also occurs on the Pacific slope at Palmar Norte in Puntarenas Province, Costa Rica, and on the Burica Peninsula between Panama and Costa Rica. It no doubt occurs as well on the Osa Peninsula in Costa Rica. It is probably restricted to premontane wet forest and tropical wet forest below 1000 m.

Birdsey (1955) reported the species to be in virgin areas in Honduras but from disturbed areas in Costa Rica. I have always found it growing in virgin forest or in disturbed remnant virgin forest but never in a weedy situation.

The species may be recognized by having leaves with numerous conspicuously sunken veins, by drying almost black, and by having juvenile blades with small, more or less spatulate lateral lobes that are directed laterally. Other distinguishing characters include the cucullate spathe blade, the sessile cup-shaped stigma, and the petiole cross-sectional shape which has an acute medial rib and conspicuously raised lateral margins.

According to Birdsey (1955) the pollen of *S. triphyllum* is unique for *Syngonium* with the "surface almost completely covered with more or less orbicular knobs."

Inflorescences have been found from February through May and in October and November. Immature fruits are known from March to October with nearly mature fruits in May, June, and July.

COSTA RICA: ALAJUELA: Vicinity of Bijauga, *Burger & Baker 9850* (F), *Croat 36268, 36484* (MO), *Utley & Utley 3906* (DUKE); NE of Villa Quesada, *Croat 46972* (MO). CARTAGO: NE of Turrialba, *Croat 43376* (MO). HEREDIA: Near Río Puerto Viejo, *Burger & Stolze 5864* (F), *Croat 35675* (MO). LIMÓN: Vicinity of Bribri, *Croat 43227, 43219* (MO); Siguirres, *Baker & Burger 188* (F); Near Tortuguero, *Davidson 6946* (MO). PUNTARENAS: Above Palmar Norte, *Allen 5929* (F), *Croat 35111, 35136* (MO). SAN JOSÉ: SW of San Isidro, *Croat 35258, 35262* (MO).

HONDURAS: ATLANTIDA: Lancetilla Valley, Near Tela, *Birdsey 319* (UC, not seen).

NICARAGUA: ZELAYA: SW of Colonia Naciones Unidas, *Stevens 4986* (MO); S of Colonia Yolania, *Stevens 4853* (MO).

PANAMA: CHIRIQUÍ: W of Puerto Armuelles, *Croat 22008, 35080* (MO). COCLÉ: Cerro Pilón, *Liesner 778* (MO); Road to Coclecito, *Croat 49228* (MO); La Mesa, *Croat 25358, 25362, 37341* (MO). COLÓN: Vicinity of Guásimo, *Croat 9939* (MO, SCZ). Río Guanche, *Croat 36999* (F, MO). VERAGUAS: NW of Santa Fe, *Croat 23118, 25643* (MO); Between Escuela Agrícola Alto Piedra and Calovebora, *Croat 23235* (F), *27572, 34142* (MO).

32. Syngonium wendlandii Schott, Oesterr. Bot. Z. 8:178. 1858. TYPE: Costa Rica, San José, Santa Ana (ca. 10 km W of San José), *Wendland s.n.* (B, now destroyed; Schott drawing 3243 seen).

Juvenile plants with stems not glaucous; internodes at first short, 2–4 cm long, becoming longer, to 10 cm long; petioles sheathed ⅓–¾ their length (usually less than ½); blades cordate, to 10 cm long, the anterior lobe ovate, acuminate, the posterior lobes semiorbicular; intermediate blades sagittate to hastate, the posterior lobes triangular, the upper surface velvety green, the major veins streaked with silver gray. Adult plants with stems green, not glaucous; internodes 1–5 cm long, 0.5–2.5 cm diam.; petioles 10–32 cm long, sheathed $^1/_2$–$^4/_5$ their length, the

free portion above the sheath acutely angled medially, the lateral margins acute; blades trisect, dark velvety green, sometimes with a streak of silver gray, the epidermis of conspicuous papillate cells; median leaflet 8–20 cm long, 2–8 cm wide, elliptic to oblong-elliptic, acuminate at the apex, acute to cuneate at the base; primary lateral veins 6–10 pairs; lateral leaflets 7–15 cm long, 3–6 cm wide, oblong-elliptic to narrowly ovate, acute to acuminate at the apex, inequilateral, the inner margin acute, the outer margin rounded to auriculate, the auricles sometimes pinched off, oblong-elliptic, to 3 cm long. *Inflorescences* 1–3 per axil; peduncles 8–10 cm long, obtusely triangular; spathe tube 5–6 cm long, 2–2.5 cm diam., narrowly ovoid, pale green outside, red inside; spathe blade elliptic, 8–10.5 cm long, acuminate at the apex, pale yellowish green outside, white inside; spadix weakly sigmoid, curved outward in the pistillate and lower part of the sterile staminate portions, then turned inward again in the upper part of the sterile staminate section; pistillate portion of the spadix 1.5–2 cm long, to 1 cm diam., the flowers irregularly 6-sided, the stigma orbicular or 2-lobed; staminate portion of the spadix white, 5.5–8.5 cm long, more or less cylindroid and markedly tapered onto the sterile staminate part of the spadix; the staminate flowers 2–4-androus (usually 4), the synandrium crenate near the apex, the area of fusion of the stamens somewhat visible; the sterile staminate flowers irregular, larger than the fertile flowers and well-spaced for the genus. *Infructescences* pendent, oblong; syncarp oblong, 2.6–5.8 cm long, 1.4–2.4 cm wide, white to brown (fide Birdsey, 1955); seeds not seen. Figs. 76–78.

DISTRIBUTION: The species is endemic to Costa Rica, occurring at about 1000 m elevation in premontane moist forest in the Meseta Central, west of the city of San José.

It can be recognized by its trisect leaves with a densely papillate upper epidermis and by its inflorescence with a frequently sigmoid spadix and widely spaced sterile staminate flowers.

The species is most easily confused with *S. hoffmannii*, a species with similar leaves that occurs at higher elevations (1500–1800 m) on the slopes surrounding the Meseta Central. The latter species is distinguished by the lack of conspicuous papillate leaf epidermis and by having a stouter spadix that is scarcely constricted at the base with the sterile staminate flowers closely compacted. Under magnification, the papillae on the upper surface of the leaf blades of *S. wendlandii* appear as minute reddish-brown glands (on dried specimens).

Birdsey (1955) is of the opinion that the leaves of the type specimens that have been photographed in Berlin were switched, with each species having its proper inflorescence but the leaves of the opposite species. (See photo FM 12299 for *S. wendlandii* and FM 12294 for *S. hoffmannii*.) The actual specimens of both species are no longer extant having been destroyed both at Berlin and Vienna; nor is the type of *S. wendlandii* among the specimens of the Wendland collection now housed at Göttingen.

I am not necessarily in agreement with Birdsey that the Berlin type photos are mixed. While the leaves of *S. wendlandii* are easily distinguishable by the conspicuous papillae on the upper leaf surface, these cannot be distinguished from the photos. The two species have leaves that are otherwise rather similar. In my opinion the leaf on the Berlin photo (FM 12294) of *S. hoffmannii* matches

FIGURES 77–80.—77. *Syngonium wendlandii* (cult. at Kew); adult blade with inflorescences.—78. *S. wendlandii*, growing at Foster Gardens; adult blades ($\times^1/_5$).—79. *S. yurimaguense*, *Prance et al. 6278*; adult plant with infructescence.—80. *S. yurimaguense*, *Ule s.n.*; adult plant with inflorescence ($\times^1/_6$).

closely the original Schott drawing (Schott Aroideae 3212) prepared at Vienna under the direction of Schott from the original (probably living) material collected by Wendland. It is possible, on the other hand, that the Berlin type photo of *S. wendlandii* (FM 12299) represents a mixed collection with perhaps a leaf of *S. hoffmannii* since this leaf does not so closely match the original Schott painting in Vienna (Schott Aroideae 3243).

COSTA RICA: ALAJUELA: Vicinity of Capulin, *Standley 40120* (US). SAN JOSÉ: Río María Aguillar, *Standley 38990* (US); *Wendland Photo #12299* (US).

33. Syngonium yurimaguense Engler, Bot. Jahrb. Syst. 38:141. 1905. TYPE: Peru, Loreto, Yurimaguas, *Ule 9237* (B, holotype; K, isotype).

Hemiepiphytic vine; stem 1–1.5 cm diam., the epidermis becoming brown, flaking; petioles slender, sheathed to upper ⅔, about as long as or to 3 times longer than the blade, 24–36 cm long, the sheath briefly free-ending and acute, the unsheathed portion acute adaxially; blades thin, trisect, the leaflets conspicuously free; median leaflet ovate-elliptic to oblong-elliptic, bluntly acute to gradually acuminate at the apex, obtuse to acute and attenuate at the base, 11–23 cm long, 4.5–9 cm wide; primary lateral veins 4–7 pairs, at least part of them departing the midrib at 90° angle, then arcuate or almost straight to the collective vein; tertiary veins distinct; primary collective vein distinct, 2–6 mm from the margin, generally more or less straight; lateral leaflets generally somewhat narrower, acuminate or narrowly acute on the inner margin at the base, hastate lobed on the outer margin, the auricles 2–5 cm long, acute to narrowly rounded at the apex. *Inflorescences* 1–2 per axil, the prophylls slender; peduncles ca. 6.5 cm long at anthesis, less than 3 mm diam. (dried); spathe 9–10 cm long; spathe tube oblong-elliptic, 3–3.5 cm long, ca. 1.5 cm diam., probably green; spathe blade oblong-elliptic, acuminate at the apex, white (fide Engler, 1877), pistillate portion of the spadix 2 cm long, 1 cm diam. (dried), the pistils depressed-globose; staminate portion of the spadix clavate, ca. 5 cm long, 7 mm diam. (dried), the sterile flowers irregular, 1–1.5 mm diam., broadest in the direction of the axis, the fertile flowers irregularly 4–5-sided, completely fused into a synandrium with no sign of fusion, the apex truncate, margin irregularly scalloped. *Infructescences* creamy yellow, subglobose, 5.5 cm long, 4.5 cm diam.; peduncle to 2 cm long; seeds black, 4–5 mm long. Figs. 79, 80.

DISTRIBUTION: *Syngonium yurimaguense* is known from Brazil, Ecuador, Peru, and Bolivia at elevations of 50 to 700 m.

It is closely related to *S. atrovirens* from western Venezuela but differs in having the spathe tube conspicuously constricted below the blade. *Syngonium yurimaguense* shares with *S. atrovirens* moderately thin leaves which have the medial lobe bearing veins which depart the midrib at almost a 90° angle. In other species of *Syngonium* the primary lateral veins depart the midrib at an acute angle.

BOLIVIA: PANDO: Cobija, Río Acre, *Ule 9237* (K).
BRAZIL: No other location, *Burchell 9859* (K). AMAZONAS: N of Ribeirão, *Prance et al. 6278* (INPA, NY, US).

ECUADOR: NAPO: N of Puyo, *Croat 49660* (MO).
PERU: CUZCO: Paucartambo, *Vargas 13426* (US). LORETO: Yurimaguas, *Ule s.n.* (B). MADRE DE DIOS: Province of Manú, *Terborgh 6739B* (F).

EXCLUDED SPECIES

Syngonium connatum Gleason, Bull. Torrey Bot. Club 56:13. 1929. TYPE: Guyana, Rupununi River, *Jenman 5756* (K, holotype) = *Philodendron hylaeae* Bunting.

Syngonium reticulatum Engler, Bot. Jahrb. Syst. 37:140. 1905. TYPE: Ecuador, San Nicolaus, *Sodiro 39* (B, holotype) = *Xanthosoma daguense* Engler.

Syngonium rothschuhianum Engler & Krause, Pflanzenr. IV. 23E (Heft 71):124. 1920. TYPE: Nicaragua, Matagalpa, 1000 m, *Rothschuh 229* (B, holotype) = *Philodendron anisotomum* Schott.

DOUBTFUL TAXA

Syngonium podophyllum Schott var. *multisectum* Engler, Pflanzenr. IV. 23E (Heft 71):129. 1920. TYPE: Based on *Duss 519* collected in a botanical garden in Martinique, previously cultivated in Buitenzorg, Java (not seen).

Syngonium sp. *Killip 5835*, consisting of part of three leaflets and lacking a petiole or any connection between the leaflets, is unusual and may represent a new species. The collection was made at La Cumbre in Colombia in the Department of Valle.

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LIFE-CYCLE VARIATION IN GEOPHYTES

Amots Dafni,[1] Dan Cohen and Imanuel Noy-Meir[2]

Abstract

Storage patterns in geophytes are integrated into one general scheme. Two patterns are recognized: geophytes in which flowers and leaves appear simultaneously (synanthous) and geophytes in which flowers and leaves appear in different seasons (hysteranthous). Within each pattern two variants can be recognized, those with annual and those with perennial storage organs. The annual developmental cycle of storage organs, of leaves, and of flowers and seeds characteristic of each type is related to ecological conditions and possible selection pressure. Large perennial storage organs are expected and found in plants of arid unpredictable areas. Hysteranthous leaves are expected to be more frequent in arid unpredictable climates.

A geophyte is a plant with a life-form in which the perennating bud is borne on a subterranean storage organ. In most geophytes the life cycle includes a dormant period that can extend from a few weeks to most of the year (Raunkiaer, 1934). Relatively few geophytes are active throughout the whole year and these are typical of the tropics (Holttum, 1955; Holdsworth, 1961).

In such a life cycle two patterns can be distinguished and in each type, annual and perennial storage organs are found: (1) Geophytes with synanthous leaves, in which leaves and flowers are simultaneous and the course of events is growth, storage, flowering and dormancy. (2) Geophytes with hysteranthous leaves, in which flowers and leaves appear in separate seasons and the course of events is growth, storage, dormancy, and flowering (Dafni et al., 1981).

Most geophytes live in and are adapted to a seasonal climate (Raunkiaer, 1934; Burns, 1946; Svoskin, 1960; Rees, 1972). A seasonal climate may also be characterized by its unpredictability. A storage organ may enable a plant to perennate in a seasonal climate, and to persist through large fluctuations in climate from year to year.

The storage organs of geophytes are able to supply food reserves for rapid leaf growth at the beginning of the season. This is typical of regions having a short photosynthetic period (Mooney & Billings, 1960, 1961; Russel, 1940, 1948; Fonda and Bliss, 1966). Storage organs may also provide reserves for growth in periods when net production is reduced. For example, food storage in bulb plants enables them to make rapid leaf growth after cold winters and/or dry summers (Rees, 1972).

In geophytes with hysteranthous leaves an accumulation of storage materials is a prerequisite for flowering (Burt, 1970).

In the literature there are few works devoted to carbohydrate concentration in geophytes throughout the year, either as the main (Mooney & Billings, 1960; Fonda & Bliss, 1966; Risser & Cottam, 1968; Ogden, 1974) or even as a minor subject (Rees, 1966, 1969, 1972; Ho & Rees, 1975; Frontanier, 1973).

The present study is an attempt to develop a single systematic treatment of the various consumption rhythms of geophytes.

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Observations and Generalizations

ANNUAL STORAGE ORGANS

Geophytes with Synanthous Leaves.—In this group the storage organ is completely renewed every year. The storage materials provide for the early growth of the photosynthetic organs. The allocation of resources for next year storage, for flowering, and for seed production may be at the expense of the storage organ or from current production.

In some Mediterranean orchids (*Ophrys, Orchis, Serapias*), the root-tuber is replaced every year, gradually increasing in size, and first flowering occurs only after five to eight years, after accumulating a minimal "critical mass," as it is well known from cultivated bulbs (see discussion). Most of the species in this group flower two to three months after the first rain. This is interpreted as a "lag period" for production and allocation of the reserve materials for the next year. A shortage of rain in this period injures mainly the current flowering and to a lesser extent the allocation for the next year. It seems that, for the survival of the genotype in unpredictable environments, the risk of injuring storage organs is more harmful than the risk of not producing flowers and seeds for one year. We assume that allocating reserves for the coming year with first priority may be considered a mechanism for achieving minimal risk. Figure 1 represents the hypothetical reserve course during the season in this group. A similar type of reserve course was found in the cultivated tulip (Rees, 1966).

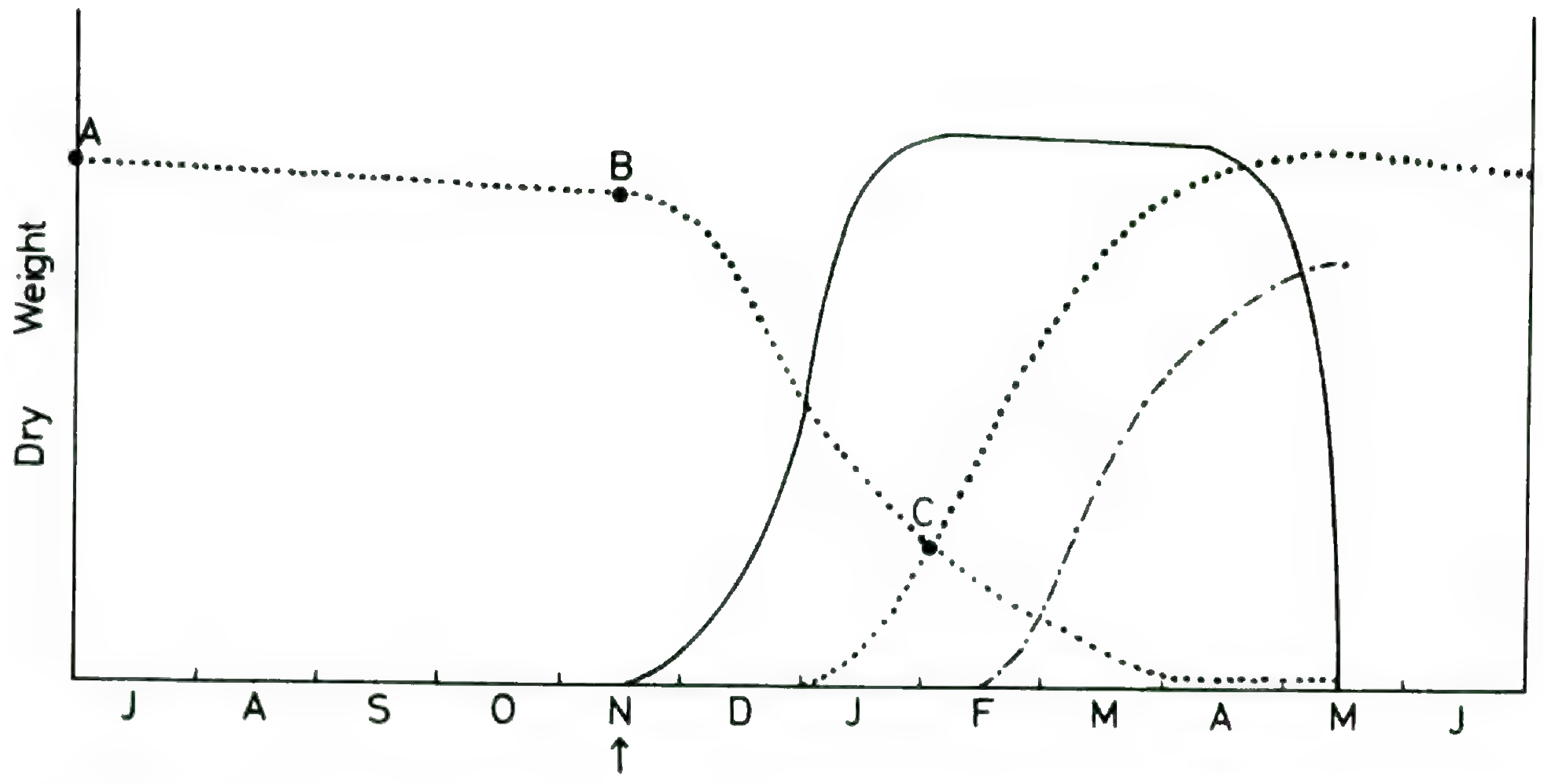
Phenological differences are summarized in two subgroups based on the speed of leaf development and the duration of the photosynthetic period.

The rapid route: Rapid leaf development may be advantangeous when the photosynthetic period is very short (Burt, 1974). The most common limiting factor is available moisture. This occurs mainly in steppes, deserts, soil pockets in rock fissures, light soils, sand dunes, etc. It may be also advantageous under conditions of high competition (Harper, 1967), when the first plant to be established is the first to succeed. The risk is that any damage to the leaves by grazing, sea spray, frost, etc. is irreparable owing to restricted reserves.

Since the productive season is very short, it is advantageous to first ensure the reserve for the coming year, and only after this to provide for the current reproductive cycle. Such a shorted and rapid development is found in *Gagea dayana* and *G. chlorantha* growing in fissures of calcarous rocks, in dry dunes and steppes in which the photosynthetic period is 2–3 months (Heyn & Dafni, 1971).

The slow route: Slow leaf production is suitable for a long photosynthetic period when the moisture, light, or temperature are not limiting factors. Typical habitats of this kind are open Mediterranean dwarf shrubs communities ("batha") with quite deep soils or field fringes. The longer exposure means greater hazards of competition.

When the leaves are active for a long period simultaneously with flowering, it is possible to allocate reserves for the coming year and for flowering at the same time, without risking survival for the next year. Because of the extended favorable conditions, current production contributes to flowering and flowering is possible even if the allocation for reserves for the coming year is incomplete,



FIGURES 1–4. Development of vegetative, reproductive, and storage organs during the year from July to June. Leaves ———. Storage organs . . . . Flowers and seeds –·–·–·–. The arrow indicates the first rain.

FIGURE 1.—An annual plant with synanthous leaves; based on data from *Serapias vomeraceae*.

because there is a reasonable chance to support seed setting from current production. Thus, we expect that the critical mass would be smaller than in the rapid route.

Slow extended flowering may be advantageous when there is a shortage of pollinators, or when a long flowering period compensates for a low number of individuals, as it is in rare species with specific pollinators (Drury, 1974) provided that there is no risk in long flowering exposures. An example is *Gagea villosa*, which grows in damp fields in the Mediterranean region in which the photosynthetic period lasts 4–6 months (Heyn & Dafni, 1977).

Geophytes with Hysteranthous Leaves.—Owing to the complete separation between the productive and consuming phases, the reserves necessary for flowering are accumulated in the previous year. If the reserves are insufficient, flowering does not occur in the following year and all the reserves are utilized to establish the photosynthetic organs. The critical mass for flowering in geophytes with an annual storage organ and hysteranthous leaves has to include the exact amount of reserves required for flowering and *seed production*, which is independent of environmental variation. This is in contrast to annuals with synanthous leaves, which risk the chance of failure in seed setting if poor conditions follow flowering.

The yearly course of accumulation and consumption of reserves is shown in Figure 2. A to B represents the preparation period in the storage organ for flowering (August–September). *B* to *C* represents expenditure on flowering and seed production. *C* to *D* represents the time interval between the end of seed production and the appearance of leaves. *D* to *E* represents expenses for leaf establishment.

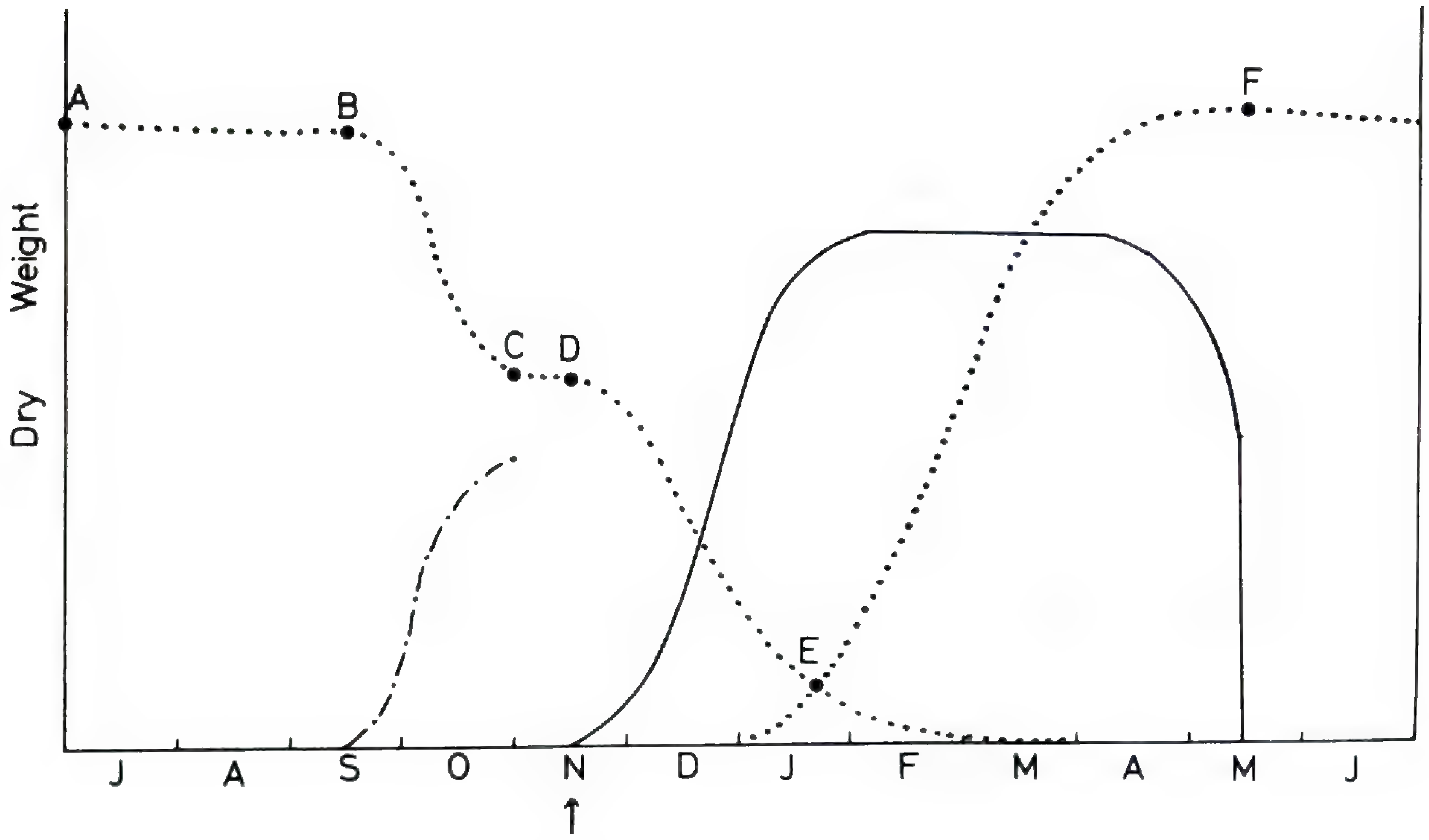


FIGURE 2.—A model of an annual plant with hysteranthous leaves.

E is the point of minimal reserve. *E* to *F* represents productive phase and allocation of reserves for the coming year (November–April).

The same routes and combinations described under the former group are also expected in this group. Flowering is completely dependent on the level of storage reached by the end of the previous year and not on current ecological conditions. Local conditions could dictate the time course of flowering. After the rains (October) one expects to find either a rapid route with a rapid production and storage, as in steppe or desert plants like *Colchicum tunicatum* and *Crocus damascenus*, or a slow route in moderate Mediterranean conditions in plants like *Colchicum hierosolymitanum* and *Crocus ochroleucus*.

PERENNIAL STORAGE ORGANS

Geophytes with Synanthous Leaves.—In perennials, the critical mass has a different significance, since the first flowering occurs only after accumulation of surplus reserves (Rees, 1972; Frontanier, 1973) so that flowering may be completed even if there is a shortage of reserves in the current year. We can suppose that in moderate and predictable habitats the "shortage fund" (the reserves above the consumption of one year) may be quite small since there are fewer chances for successive bad years. In extreme and unpredictable habitats, there is a greater chance for successive dry years, and it is expected that the first flowering would occur only after the allocation of a large "shortage fund." This "fund" has to be sufficient to support several successive years of shortage, so that flowering may be expected to occur every year. Our field observations support the suggestion that if the storage organ is large enough, indicating a large "shortage fund," flowering will occur almost every year. It should be borne in mind that the re-

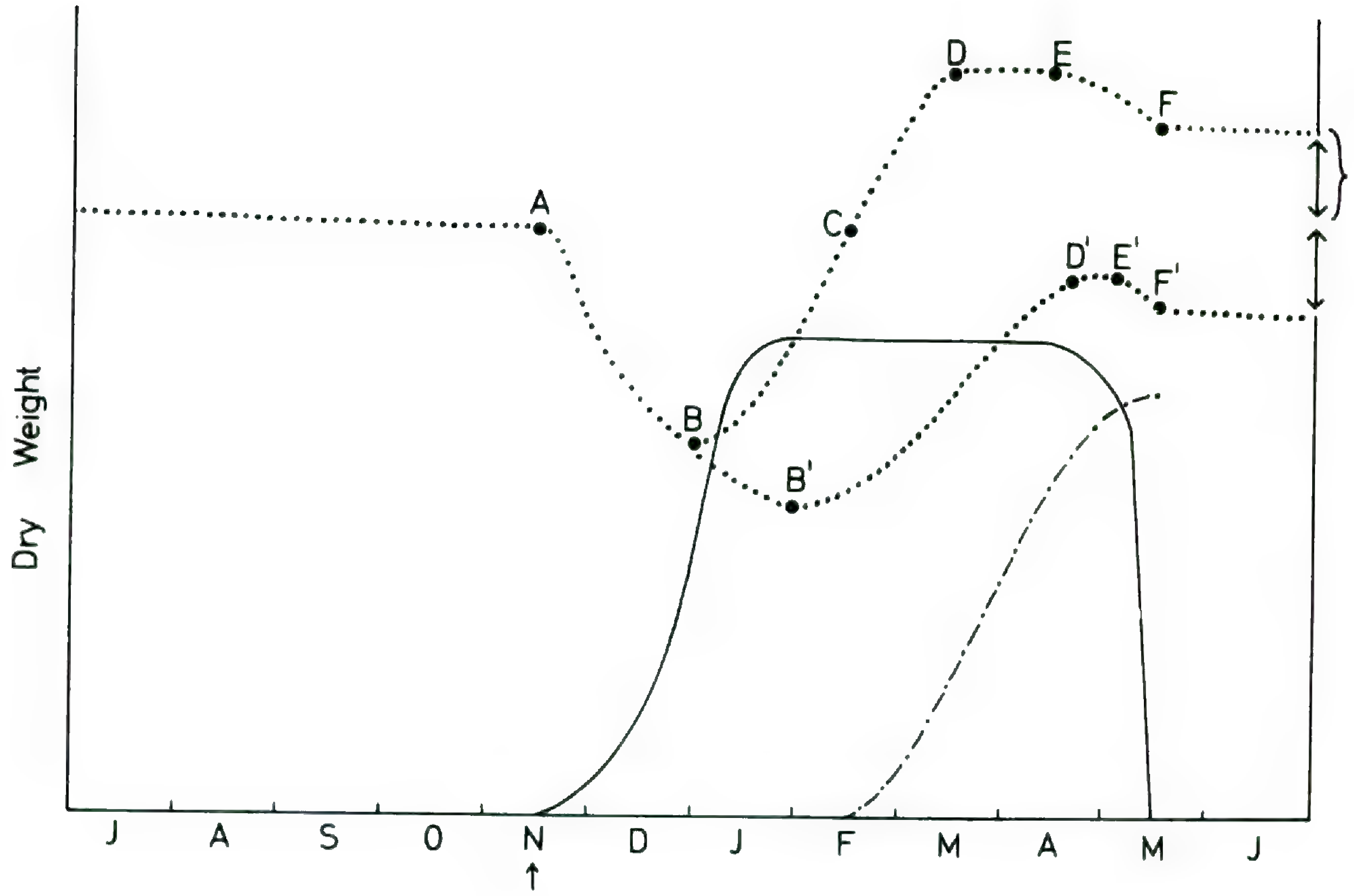


FIGURE 3.—A model of a perennial plant with synanthous leaves.

serves are not the only conditions for flowering and that other triggers like the temperature regime can be very important (Hartsema, 1961; Rees, 1966). Species with large reserves which flower almost every year are: e.g., *Scilla hyanthoides, Cyclamen persicum, Lilium candidum*, and many others.

The yearly course of accumulation and consumption of reserves is shown in Fig. 3. In a good year (*A–F*), the following phases could be distinguished: *A* to *B*, expenses for leaf establishment until net production occurs; *B* to *C*, the "store walls" plus the "shortage fund"; *C* to *D* the beginning of flowering and continuation of net production; *D* to *E* the balance period between the expenditure and production; *E* to *F* the expenditure for flowering plus seed production is greater than the production; *A* to *F* is the profit of the current season added to the "shortage fund." In a "bad year" (*A–F'*): *A* to *B'*, the expenditure period for leaf establishment, is longer than *A–B* and the rate of net production accumulation is slower. *A* minus *F'* is the shortage of the current year.

A similar type of reserve course was found in cultivated *Narcissus* (Grainger, 1941), *Polygonum bistortoides*, and *Geum turbinatum* (Mooney & Billings, 1960) and in two species of *Erythronium* and of *Dicentra* (Risser & Cottam, 1968).

The rapid and slow secondary routes are also expected in this group.

The rapid route can be a possible adaptation to extreme habitats in which annual geophytes cannot exist and which can only be occupied for a short time. For example, in *Polygonum bistortoides*, which grows in the extreme tundra, 50% of its total reserves were utilized in one week (Mooney & Billings, 1960). A rapid growth cycle also exists in *Erythronium* and *Dicentra* species which grow in a forest of sugar maple and basewood beech (Risser & Cottam, 1968) during

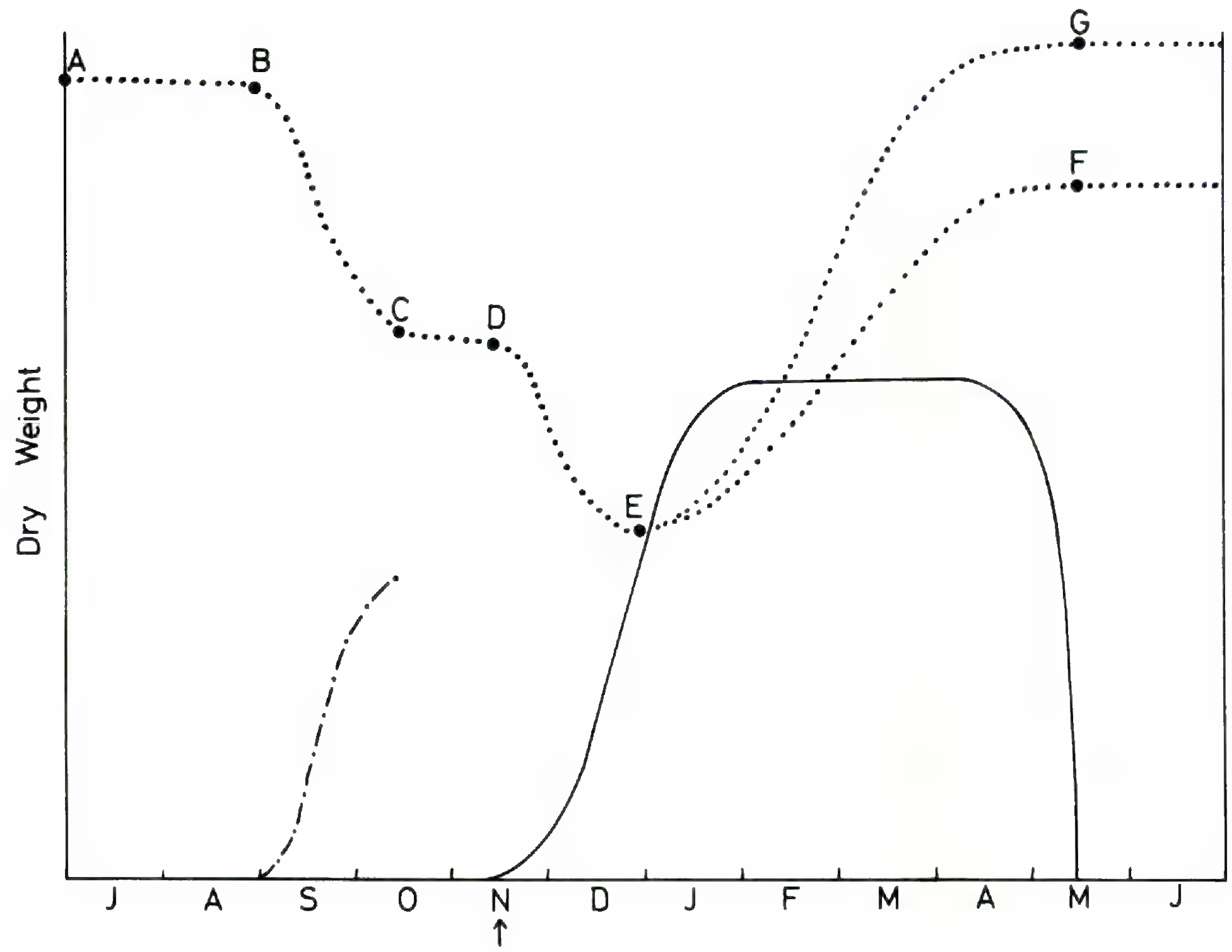


FIGURE 4.—A model of a perennial plant with hysteranthous leaves.

a short period of photosynthesis in the spring, before the tree leaves develop, and also in *Carex bigelowii* from alpine regions with short growth season (Fonda & Bliss, 1966).

The slow route is found in habitats which permit a long season of growth. In typical Mediterranean conditions five to six months of continuous growth are possible. Many geophytes expand their leaves after the first rains but flower only in late winter or in the spring, e.g., *Lilium candidum, Scilla hyanthoides, Ranunculus asiaticus, Asphodellus microcarpus,* and many others.

Perennial Geophytes with Hysteranthous Leaves.—In this group flowering and storage of new reserves occur in different seasons. The abundance of flowering can only be influenced to a limited extent by the current climatic conditions. After the accumulation of the initial critical mass, flowering can occur almost every year. It is expected that only slight differences will be found in the abundance of flowering from year to year.

The hypothetical reserve course during the season (Fig. 4) is similar, in principle, to that of annuals with hysteranthous leaves (Fig. 2), with one major difference—the existence of a "shortage fund" plus the "store walls." In a good year, a surplus (Fig. 4, *A–G*) is added to the "shortage fund" and, in a bad year, the deficit is taken from the shortage fund (Fig. 4, *A–F*). The course of development up to the next leaf production can be the same in good or bad years, since flowering is independent of concurrent climatic conditions.

Fast and slow secondary routes are similar to those in the other groups. In *Scilla hunburyi*, which grows in steppes, the leaves are active for about two months; in *Scilla autumnalis*, which grows in the Mediterranean area, the photosynthetic season lasts 3 to 4 months, in *Urginea maritima* for about 8 months and in *Pancratium maritimum* about 9 months. The growth season seems to correspond to the availability of moisture. Vegetative growth varies widely between years, but flowering occurs every year.

Discussion and Conclusions

It is well known from horticultural practice that bulbs and corms below a certain size do not flower. There appears to be a minimum size of storage organ in each species and variety for flowering to occur (Rees, 1969, 1972). Frontanier (1973) notes that the juvenile period in bulbs and corms varies from one to seven years and that this variation can be related to the minimum bulb weight. Considering that all this evidence was collected under predictable agricultural conditions, it is quite reasonable to assume that the size of the reserve is the major regulating factor and that after the first flowering, flowering is expected to occur every year. In a natural unpredictable environment, plants must be more flexible in order to prevent flowering in a bad year as a means of escaping starvation at the end of the season and primarily to ensure the next vegetative phase.

Geophytes growing in a seasonal climate with a restricted growth period, must have a more complicated use of reserves in order to reduce risks. Frontanier (1973) stresses that when the time between initiation and flowering in cultivated bulbs is long, one must distinguish between a minimal reserve for the initiation of flowering and a second amount of reserves for flower development. According to his data, it can be concluded that the bulb size is more important in geophytes in which the initiation of flowering occurs during the storage period (e.g., *Tulipa, Crocus*), than in those in which the initiation of flowering occurs after planting (e.g., *Lilium, Allium*).

Since an annual pattern is more opportunistic than a perennial pattern due to the lack of a "shortage fund," one expects to find fewer annual geophytes than perennial geophytes in deserts and steppes. Since the life cycle of annual geophytes with hysteranthous leaves is less risky than the life cycle of those with synanthous leaves, due to the separation of phases, it is reasonable to find relatively more representatives of the first group in arid environments. Thus, it is expected to find relatively larger storage organs under arid conditions, compared with those from mesophytic environments, and that the storage organs of geophytes with hysteranthous leaves would be larger than those with synanthous leaves, because of the need for keeping a larger "shortage fund." The first prediction was confirmed by Shimshi (1972) in the genera *Crocus, Colchicum*, and *Tulipa*, and there are more examples in *Scilla* and *Pancratium*; so far there is no information about the second prediction.

It is expected that the fraction of the whole perennial reserve devoted to flowering will be smaller in unpredictable regions.

In all cases, a strategy that requires a larger amount of storage material will be favored by a high conversion efficiency of the reserves and a low maintenance cost of the storage organs (Cohen, unpublished).

Perennial geophytes with hysteranthous leaves require larger reserves, and it is expected that the efficiency of utilization of reserve materials will be greater than in those with synanthous leaves and that the maintenance costs are lower in the former.

If the storage costs are high, it is expected that at least some of the leaves would be produced at the expense of current production and not out of reserves. Such a situation can be revealed by comparing the allocation of reserves for leaf production with the decline of the reserve in the storage organ (Rees, 1972:47; Grainger, 1941).

To summarize, the following conclusions can be drawn:

1. Two main patterns can be defined in geophytes: those with a perennial storage organ; and those with an annual storage organ which is completely renewed every year. In each group there are two main routes: a rapid route and a slow route with short and long periods of vegetative growth.

2. In annual geophytes with synanthous leaves, flowering will take place only after the accumulation of a minimal reserve during the photosynthetic period. This mass is termed "the critical mass." The most environmentally dependent phase would be seed production, since it seems that this phase needs additional reserves from current production. In a poor year, flowering and, especially seed production, would be very poor, if it occurred at all, due to failure to reach the "critical mass." In perennials the accumulated reserve is greater than the requirement for one year, and it is termed the "shortage fund." This reserve enables completion of flowering and seed production even if the net production that year is insufficient to complete it. Therefore relatively slight differences are expected from year to year in the abundance of flowering.

3. In annual geophytes with hysteranthous leaves, the reserve accumulated in one year must provide for flowering, seed production and leaf establishment of the next year. Annuals depend on environmental fluctuations, and if the "critical mass" is not accumulated, then flowering cannot occur. However, if it does occur, full seed production is expected, because the critical mass includes almost all the requirements for seed production also.

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NEW TAXA IN *PIPTOCARPHA* R. BR. (VERNONIEAE: COMPOSITAE)[1]

GERALD L. SMITH[2]

ABSTRACT

The general distribution and striking features of *Piptocarpha* are discussed. Three new species and one subspecies are described and figured: *Piptocarpha jonesiana* G. L. Smith and *P. opaca* (Benth.) Baker subsp. *piraparanäensis* G. L. Smith from southeastern Colombia; *P. barrosoana* G. L. Smith and *P. prancei* G. L. Smith from Brazil.

A neotropical genus of approximately 45 species, *Piptocarpha* extends from southern Brazil and northern Argentina into the West Indies and Central America. The major center of distribution is southern and eastern Brazil but secondary centers are the northern and central Andes, the Venezuelan Guayana Highland and the Amazon River Basin.

Striking field features of the genus are the axillary inflorescences, which frequently take the form of dense globose glomerules, and the scandent habit of many species. The scandent species usually form dense thickets or climb high in trees. Other species are trees, these largely distributed in the highlands of southern Brazil.

Important contributions to our understanding of *Piptocarpha* in the twentieth century have been made from Colombia by Cuatrecasas (1955), from Venezuela by Aristeguitea (1964, 1967), and from Brazil by Barroso (1959, 1969) and Cabrera (1961, 1964). These treatments have been of considerable value in the comprehensive revision of *Piptocarpha*, currently in progress at the University of Georgia. As some time must elapse before my full revision is published, I here describe one new species and one subspecies from Colombia and two new species from Brazil.

Piptocarpha jonesiana G. L. Smith, **sp. nov.**—FIG. 1. TYPE: Colombia. Vaupés-Amazonas: Río Apaporis, Raudal Yayacopi (La Playa) and vicinity, alt. 800 ft, 18 Aug. 1952, *Schultes & Cabrera 16888* (GH!, holotype; US!, isotype). PARATYPES: Colombia. Vaupés-Amazonas: Jino-Gogé, 26 Aug. 1952, *Schultes & Cabrera 17035* (GH!, NY!, US!); 25–26 Aug. 1952, *García-Barriga 14226* (US!).

Frutex scandens, ramis cinereo-lepidoto-tomentellis. Folia alterna 3–7 × 1–1.5 cm, subcoriacea, ovala vel anguste lanceolata, supra glabra, infra dense cinereo-lepidota; petioli 3–4 mm longi. Inflorescentiae axillares corymbosae vel paniculatae glomeratae. Capitula 5–6-flosculosa, pedunculi brevi, tomentosi; involucrum anguste campanulatum 6–7 × 3–4 mm; phyllaria irregulariter imbricata 3–4-seriata, brunnea in sicco, ad apicem maculata. Corollae albae, tubo 3.5–4 mm longo, lobis 1.5–2 mm longis; antherae 3.5–4 mm longae, auriculae basi argute caudatae 0.5 mm longae. Pappi albi, biseriati,

[1] I wish to thank Dr. Samuel B. Jones, Jr. for the opportunity of doing the challenging revision of *Piptocarpha*; Nancy Coile, Curator of GA Herbarium for securing the herbarium loans; Marvin Sexton and Geneva Rice for preparing the figures; and Carla Ingram and Kim Garrett for typing the manuscript.

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FIGURE 1. A. Holotype of *Piptocarpha jonesiana* G. L. Smith. B. Inflorescence of A.

setae interiores filiformes ca. 5.5 mm longae, setae exteriores lineares 0.5–1.5 mm longae. Achaenia ca. 3.5 mm longa, sparsim pilosa, interdum 4-angulata, 10-costata.

Scandent *shrub*, main branches 3–6 m long, terete, faintly striate, cinereous lepidote-tomentulose, lateral branchlets numerous, short. *Leaves* somewhat crowded along the branches; petioles short, closely and densely cinereous-to-mentose-lepidote 3–5 mm long; blades small, 3–7 × 1–1.5 cm, subcoriaceous, oval to narrowly lanceolate, glabrous above, with reticulate venation prominent, cinereous-lepidote beneath, with 5–6 lateral veins on each side, acute at apex or occasionally mucronate, slightly oblique to narrowly rounded at base, margins entire and slightly revolute. *Inflorescences* axillary, of 5–15 heads, corymbose or paniculate. *Heads* of 5–6 florets, borne on short tomentose peduncles along and at the end of rachises; involucre narrowly campanulate 6–7 × 3–4 mm; phyllaries irregularly imbricate in 3–4 series, brown with dark tips, the outer ones ovate, tomentulose and subobtuse at apex, marginally arachnoid, the inner ones oblong, glabrate, subacute or obtuse at apex, minutely ciliate. *Corrollas* white, with scattered glands at the juncture of the lobes and tube, tube 3.5–4 mm long, the lobes 1.5–2 mm long; anthers 3.5–4 mm long, the basal auricles sharply caudate ca. 0.5 mm long. *Pappus* white, biseriate; inner bristles numerous, filiform ca. 5.5 mm long, outer bristles few, linear 0.5–1.5 mm long. *Achenes* ca. 3.5 mm long, sparsely pilose, occasionally 4-angled, 10-costate.

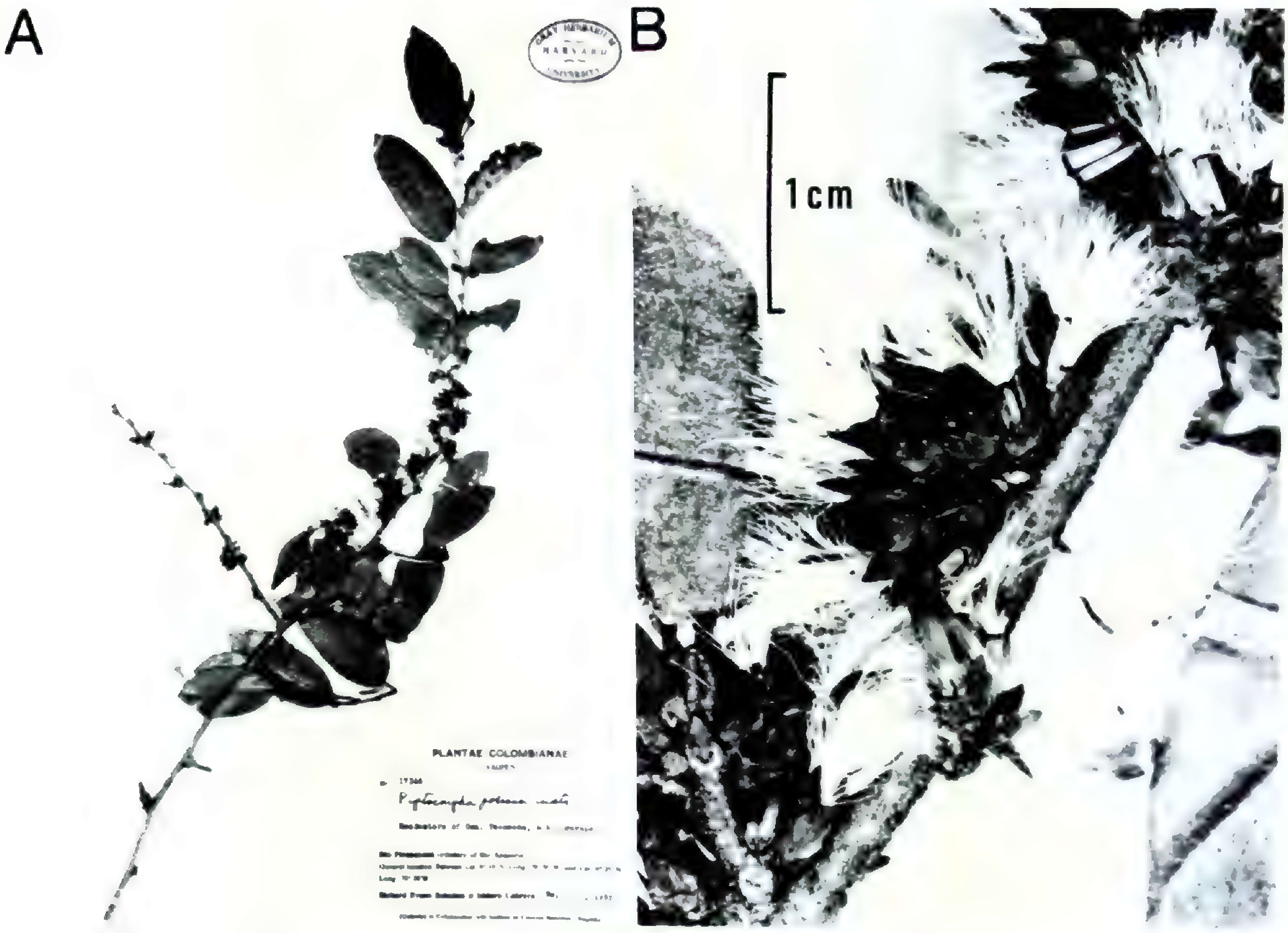

FIGURE 2. A. Holotype of *Piptocarpha opaca* (Benth.) Baker subsp. *piraparanäensis* G. L. Smith. B. Inflorescence of A.

Piptocarpha jonesiana is distinguished by its small oval or narrowly lanceolate leaves and by its shortly paniculate to corymbose inflorescences. It is distributed along the Río Apaporis between Deptos. Vaupés and Amazonas in southeastern Colombia at elevations near 300 m as a shrub climbing in trees; it flowers and fruits chiefly in August and September. This species is named in honor of Dr. Samuel B. Jones, Jr. a major contributor to the taxonomy of the Vernonieae.

Piptocarpha opaca (Benth.) Baker subsp. **piraparanaënsis** G. L. Smith, **subsp. nov.**—FIG. 2. TYPE: Colombia. Vaupés: Río Piraparaná headwaters of Cãno Teemeeña, Lobo Igarapé, 10 Sep. 1952, *Schultes & Cabrera 17346* (GH!, holotype; BM!, NY!, US!, isotypes). PARATYPES: Colombia. Vaupés: Río Piraparaná, 5 Sep. 1952, *Schultes & Cabrera 17198* (NY!, US!); along airstrip at Mitú, 18 May 1976, *Zarucchi 1598* (US!).

Folia alterna 5–8.5 × 2–3 cm, coriacea, oblonga vel elliptica, supra glabra, infra cinereo-tomentosa, pilis stellatis; petioli 5–10 mm longi. Inflorescentiae axillares hemisphaericae glomeratae. Capitula 6–8 flosculosa, subsessilia; involucra turbinata 7.5–8 × 3.4 mm.

Leaves with petioles furrowed, cinereous-tomentose 5–10 mm long; blades usually small 5–8.5 × 2–3 cm, with 4–7 lateral veins on each side. *Inflorescences* axillary, hemispheric clusters of 7–9 heads. *Heads* of 6–8 florets, subsessile; involucre turbinate 7.5–8 × 3–4 mm.

This subspecies is distinguished from the subspecies *opaca* by smaller oblong

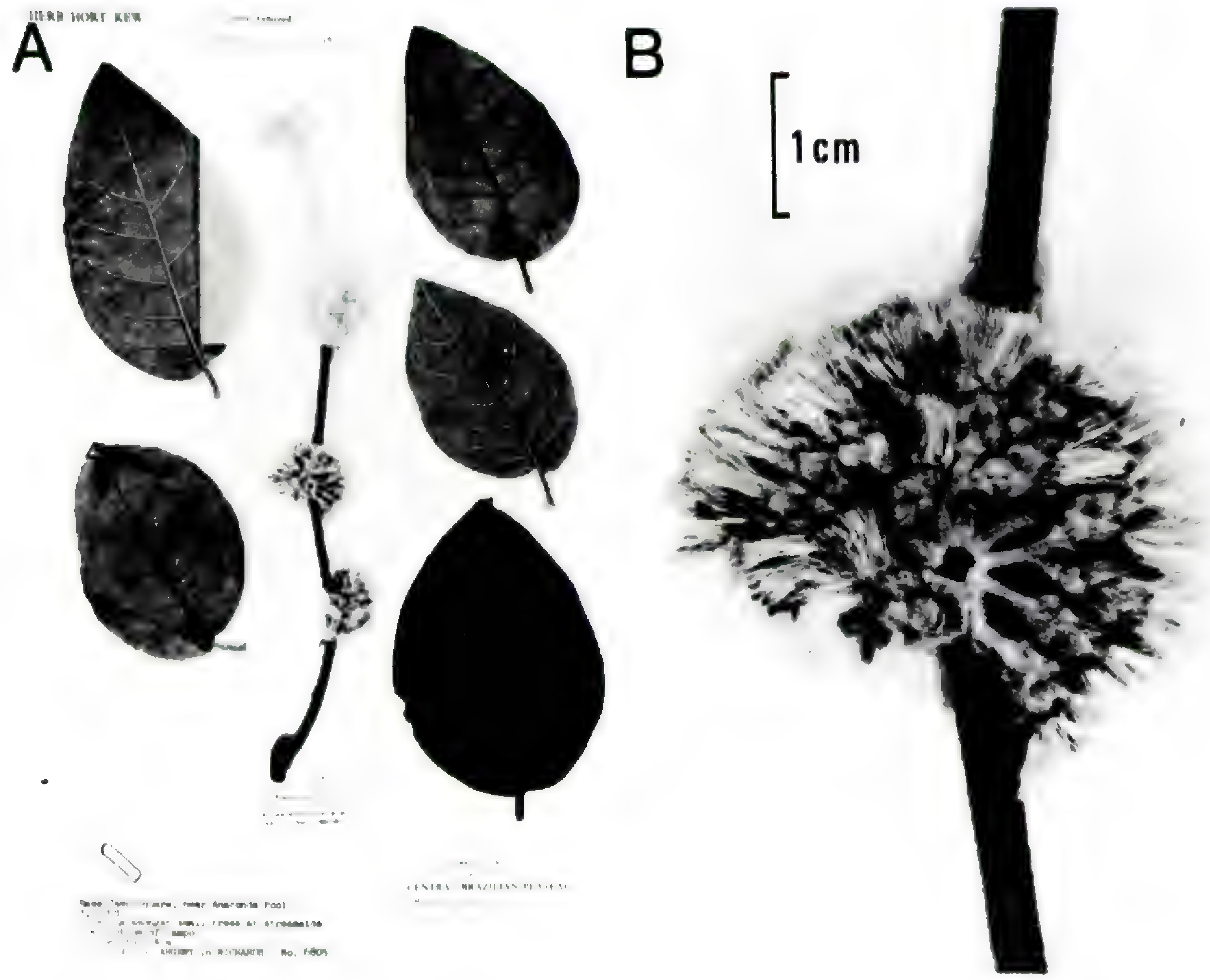

FIGURE 3. A. Isotype of *Piptocarpha barrosoana* G. L. Smith. B. Inflorescence of A.

or elliptic leaves and smaller heads. It is distributed along and near the margins of the Río Piraparaná as a shrub climbing in trees and forming riverine thickets; it flowers and fruits chiefly from May to September.

Piptocarpha barrosoana G. L. Smith, **sp. nov.**—FIG. 3. TYPE: Brazil. Mato Grosso: Serra do Roncador, Base Camp Square near anaconda pool, 31 Aug. 1968, *Argent in Richards 6805* (RB!, holotype; E!, K!, NY!, isotypes).

Frutex scandens, ramis cinnamomeo-tomentosis. Folia alterna 8–13 × 4–7.5 cm, subcoriacea, ovata vel suborbiculata, supra subrugosa scabra, costa tomentosa, infra argenteo-cinereo-tomentosa, pilis stellatis et pedicellatis; petioli 10–30 mm longi. Inflorescentiae axillares globose corymbosae glomeratae. Capitula 6-flosculosa, sessilia vel breviter pedicellata, solitaria vel bina aggregata, pedunculis argenteo-tomentosis; involucrum ovoideum vel campanulatum 6–7 × 3.5–4.5 mm; phyllaria arcte imbricata 3–4-seriata, persistentia, argenteo-tomentosa sed ad apice flavo-tomentosa. Corollae verosimiliter albae, tubo ca. 4.5 mm longo, lobis 1.5–2 mm longis; antherae ca. 3.5 mm longae, auriculae basi argute caudatae 0.5 mm longae. Pappi albi, imprimis uniseriati, setae interiores filiformes 6–6.5 mm longae, setae exteriores paucae minus quam 1 mm longae. Achaenia 4 mm longa, 10-costata, glandulifera.

Scandent *shrub*, the main branches up to 4 m long, terete, cinnamon-tomentose; lateral branchlets numerous, short, with axillary flowering glomerules. *Leaves* evenly spaced along the branches; petioles cinnamon-tomentose, 10–30 mm long; blades large, 8–13 × 4–7.5 cm, somewhat coriaceous, ovate to suborbicular, subrugose, scabrous above, the midvein tomentose, silvery-gray-tomen-

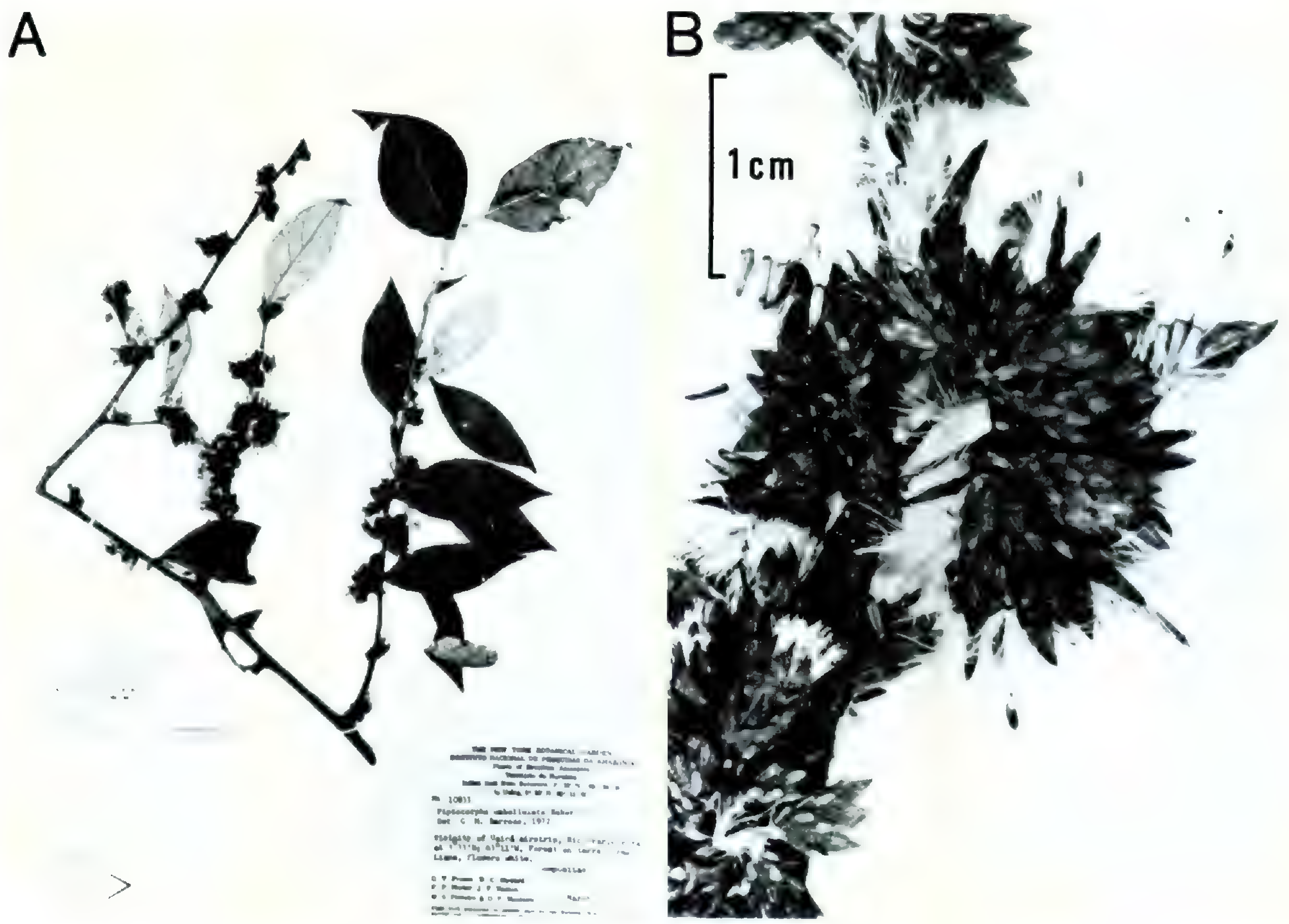

FIGURE 4. A. Isotype of *Piptocarpha prancei* G. L. Smith. B. Inflorescence of A.

tose with stalked stellate trichomes beneath, with 6–8 prominent lateral veins on each side, acute at apex, slightly oblique to cordate at base, the margins entire. *Inflorescences* axillary, globose, corymbose clusters of 10–30 heads. *Heads* of 6 florets, sessile or shortly pedicillate, solitary or paired on silvery-gray-tomentose peduncles; involucre ovoid to campanulate, 6–7 × 3.5–4.5 mm; phyllaries imbricate in 3–4 series, persistent, silvery-tomentose but yellow-tomentose at apex (the inner ones glabrous below middle), the outer ones ovate, subacute at apex, the inner ones oblong, abruptly acuminate at apex. *Corollas* probably white, occasional glands at the juncture of the tube and lobes and on the outer surface of apically pilose lobes, the tube ca. 4.5 mm, the lobes 1.5–2 mm long; anthers ca. 3.5 mm long, basal auricles sharply caudate ca. 0.5 mm long. *Pappus* white, chiefly uniseriate; inner bristles numerous, filiform 6–6.5 mm long, outer ones few, inconspicuous, less than 1 mm long. *Achenes* 4 mm long, 10-costate, gland-dotted.

Piptocarpha barrosoana is one of the most distinctive and striking species in the genus. It is easily distinguished by its silvery-tomentose involucres and cinnamon-tomentose branchlets and is most closely allied to species with a chiefly uniseriate pappus, prominently 10-costate achenes and an ovoid to cylindrical involucre. This species is known only from the Serra do Roncador in northeast Mato Grosso. It is found climbing among trees in gallery forests; it flowers and fruits chiefly in August and September. This species is named in honor of Dr. Graziela M. Barroso, Senior Taxonomist of the National Botanical Garden, Rio de Janeiro and specialist in Brazilian Compositae taxonomy. Dr. Barroso has

provided much assistance to me, John Stutts and Nanda MacLeish during expeditions to Brazil. I am grateful for her kind support and encouragement.

Piptocarpha prancei G. L. Smith, **sp. nov.**—FIG. 4. TYPE: Brazil. Territorio Roraima: vicinity of Uaicá airstrip, Rio Uraricoeira, 2 Mar. 1971, *Prance, Steward, Harter, Ramos, Pinheiro & Monteiro 10833* (RB!, holotype; F!, K!, NY!, S!, US!, isotypes).

Frutex scandens, ramis cinereo-lepidoto-tomentellis. Folia alterna 5–9 × 2–3.5 cm, coriacea, elliptica, supra glabra, infra cinereo-tomentosa, pilis stellatis et breviter pedicellatis. Inflorescentiae axillares corymbosae vel subumbellatae glomeratae. Capitula 8–9-flosculosa, sessilia vel breviter pedicellata, pedunculis gracilibus plerumque inter se aequilongis; involucrum anguste campanulatum ca. 9 × 4–5 mm; phyllaria arcte imbricata 6–7-seriata, tota brunnea in sicco; flosculi paleis deciduis lineari-lanceolatis subtenti. Corollae albae, tubo 4–4.5 mm longo, lobis 1.5–2 mm longis; antherae ca. 3 mm longae, auriculae basi argute caudatae ca. 0.4 mm longae. Pappi albi, imprimis uniseriati, setae interiores filiformes 5–5.5 mm longae; setae exteriores paucae filiformes minus quam 1 mm longae, achaeniorum nonnullarum deficientes. Achaenia 2.5–3 mm longa, interdum 3-angulata, indistincte costata.

Scandent *shrub*, branches long, pendulous, terete, cinereous-tomentulose-lepidote, lateral branchlets numerous, short, with axillary flowering glomerules. *Leaves* evenly spaced along the branches; petioles furrowed, cinereous-tomentulose-lepidote 5–15 mm long; blades 5–9 × 2–3.5 cm, coriaceous, elliptic, glabrous, finely reticulate above, cinereous-tomentose with shortly stalked stellate trichomes beneath, with 5–6 prominent lateral veins on each side, acuminate at apex, cuneate at base, margins slightly revolute and remotely denticulate. *Inflorescences* axillary, corymbose to subumbellate clusters of 6–18 heads. *Heads* of 8–9 florets, sessile or shortly pedicillate on slender peduncles usually of uniform length; involucre narrowly campanulate, ca. 9 × 4–5 mm; phyllaries closely imbricate in 6–7 series, uniformly brown when dried except slightly darkened and acute at apex, ciliate, the outer ones triangular-ovate, tomentulose-lepidote at apex, the inner ones oblong to lanceolate; florets subtended by linear-lanceolate chafflike phyllaries, deciduous with achenes. *Corollas* white, glabrate, the tube 4–4.5 mm long, the lobes 1.5–2 mm long; anthers ca. 3 mm long, basal auricles sharply caudate ca. 0.4 mm long. *Pappus* white, chiefly uniseriate; the inner bristles numerous, filiform, 5–5.5 mm long, outer bristles few, filiform, less than 1 mm long, totally absent on some achenes. *Achenes* 2.5–3 mm long, occasionally 3-angled, indistinctly costate.

Piptocarpha prancei is distinguished by coriaceous, elliptic leaves with cuneate base and by subumbellate inflorescences and is most closely allied to species with sharply caudate anther tails and florets subtended by chafflike phyllaries. It is distributed in Territorio do Roraima along the margins of the Rio Uraricoeira as a shrub climbing in trees of forest on terra firme; it flowers and fruits chiefly in February and March. This species is named in honor of Dr. Ghillean T. Prance, Vice President and Director of Botanical Research, The New York Botanical Garden. Dr. Prance's many fine collections have been of great value to the workers in Vernonieae taxonomy at the University of Georgia and his assistance in planning my field work in Brazil is gratefully acknowledged.

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HAPLOMITRIUM MONOICUM, A REMARKABLE NEW SPECIES OF CALOBRYALES (HEPATICAE) FROM NEW CALEDONIA, TOGETHER WITH A RECLASSIFICATION OF SUBG. *HAPLOMITRIUM*[1]

JOHN J. ENGEL[2]

ABSTRACT

Haplomitrium subg. *Haplomitrium* is circumscribed to include the following four species: *H. hookeri*, *H. ovalifolium*, *H. intermedium*, and the newly described *H. monoicum* Engel. The last possesses a combination of unique features that taxonomically isolate it. Among these are: whitish antheridia with highly abbreviated stalks that gradually merge with the antheridial body; antheridia and archegonia 1–2 per bract; the monoecious condition; bordered leaves; lack of leaf slime papillae; and the striolate-papillose cuticle. *Haplomitrium monoicum* is placed in a new section, sect. *Protohaplomitrium* Engel and is endemic to New Caledonia.

The genus *Haplomitrium* consists of some 12 species. The genus is rather widespread in distribution, but the species are, for the most part, restricted in range, as follows: *H. ovalifolium* Schust. (Campbell Is., New Zealand); *H. gibbsiae* (Steph.) Schust. [New Zealand, Tasmania (leg. Engel)]; *H. intermedium* Berrie (Australia, New South Wales); *H. blumii* (Nees) Schust. [Java, Sumatra, New Guinea, Taiwan (Inoue, 1974), Eastern Himalayas of India (Udar et al., 1968)]; *H. giganteum* (Steph.) Grolle (Philippines); *H. mnioides* (Lindb.) Schust. (Japan, Taiwan); **Haplomitrium dentatum** (Kumar & Udar) Engel, comb. nov. (basionym: *Calobryum dentatum* Kumar & Udar, J. Indian Bot. Soc. 55:23. 1976) plus *H. grollei* Kumar & Udar and *H. indicum* (Udar & Chandra) Schust., all from the Darjeeling region of India; *H. hookeri* [Europe, Spitzbergen, W. Greenland, Eastern North America, Western North America (Schofield, 1968; Worley, 1969), Japan (Inoue, 1971), Eastern Himalayas of India (Udar & Chandra, 1965a), Western Himalayas of India (Udar & Singh, 1977)]; *H. chilensis* Schust. (southern South America); and *H. andinum* (Spruce) Schust. (neotropics, ranging from Andean Peru and Ecuador to Lesser Antilles). Marshall R. Crosby recently collected a specimen in New Caledonia that proved to be a critical new species. This is described below.

Haplomitrium monoicum Engel, sp. nov.

Planta monoica. Folia plerumque elliptica, ad apicem pro parte maxima late rotundata; margines integrae, non repandae lobatae vel dentatae. Papillae mucigerae foliorum maturarum atque immaturarum nullae. Cellulae marginales foliorum uniseriatae, medianis grandiora et parietibus crassioribus; medianae 54–70 μm latae, 55–78 μm longae; cuticula foliorum striolato-papillosa.

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Antheridia archegoniaque ad apicem axis vel prope hunc posita, 1–2 per bracteam, non in distinctum receptaculo termini aggregata. Antheridia matura eburnea, anguste ovoidea vel ellipsoidea; pedicellus 1–2 cellulae longus, crassus, a corpore antheridii vix distinctus.

TYPE: NEW CALEDONIA. Montagne des Sources Reserve, ca. 20 air-km NE of Nouméa, 750 m, 3 September 1981, *Crosby 14165* (F, holotype; NOU, PC, PE, isotypes).

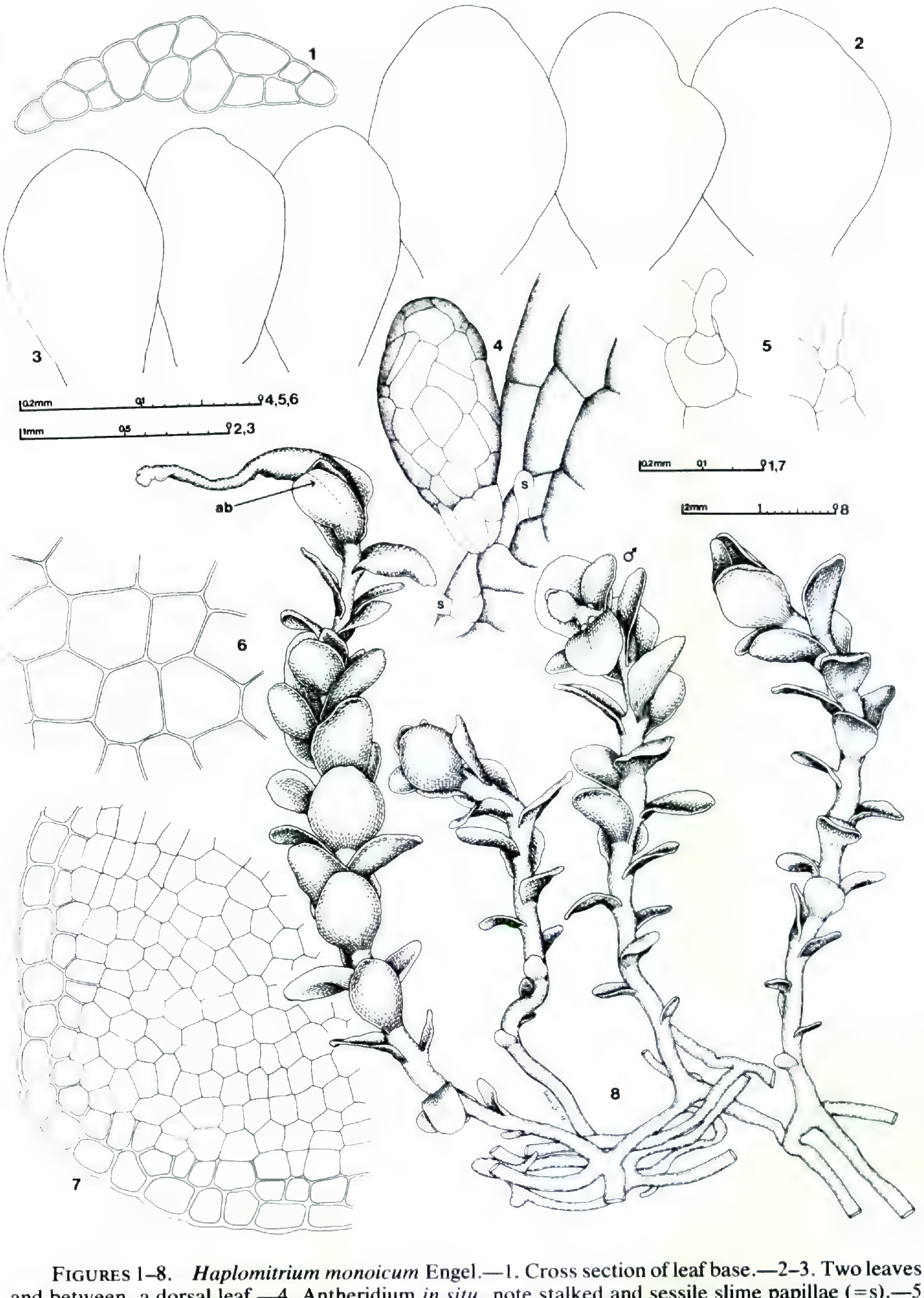
Plants fleshy, brittle, pure grass green, small, the sterile leafy shoots 1.2–1.8 mm wide, 5.4–8 mm high, isophyllous or subisophyllous and arising from a system of prostrate, pale or whitish, leafless, elongated, often ramified, basal rhizome, the rhizome sometimes gradually converted into erect, leafy axes; geotropic, leafless stolons from leaf axils and terminal furcate branching both lacking; erect shoots for most part leafy throughout, only a comparatively short, basal region naked. *Leaves* (mature) of sterile shoots subequal in size from shoot base to apex, the nodes at ± regular intervals; leaves bistratose in a small but distinct median-basal field, the marginal 1–2 cell rows unistratose, the remainder of leaf otherwise unistratose; lateral leaves transversely to subsuccubously oriented and inserted, the dorsal leaves remaining transversely so, at least on well-developed shoots; leaf insertion often slightly acroscopically arched. Leaves erect-spreading to spreading at ±90°, remote to approximate, plane or becoming gently and gradually deflexed, longer than broad, usually elliptic, less often feebly obovate or suborbicular, rather narrowed at the base; apex mostly broadly rounded, sometimes narrowly so; margins plane and not sinuous, entire. Dorsal leaves generally a little smaller and narrower than lateral leaves, the dorsal leaves at times somewhat irregular in shape, at times not perceptibly differing from lateral leaves. Leaves toward base of shoot much reduced, the proximal ones scalelike, but within ca. 2–3 leaf cycles becoming linear, then oblong prior to the mature condition. Slime papillae lacking on both leaf margins and surface. Leaves bordered by 1(–2) rows of larger cells with thicker walls than the internal ones, the marginal cells 46–55(–66) μm wide, 54–73(–78) μm long, averaging 1.1–1.7 times area of the interior adjacent cells; intramarginal cells leptodermous, large for genus, those in median portion of leaf 54–70 μm wide, 55–78 μm long; cuticle striolate–minutely papillose. *Plants monoecious*; male plants ± same size as sterile or gynoecial shoots, the plants not heterothallic. *Antheridia* near or at summit of shoot and not generally dispersed along axis; perigonal bracts similar to leaves; antheridia 1–2 per bract, confined to the bract axil, appearing almost sessile, whitish green ripening to ivory white (the post-dehiscence antheridia pale brown), narrowly ovoid to elliptic, with stalk 1–2 cells long, gradually grading into body, the jacket cells large; slime papillae interspersed with antheridia, the papillae either sessile or mounted on a stalk of 1 cell, the slime cell linear to elongate subclavate; antheridial terminal disc not differentiated, although the shoot apex at times becomes slightly dilated with androecial formation; swollen fertile "nodes" and subsequent apical innovation absent. *Archegonia* red brown with age, with position and number similar to antheridia: the archegonia 1–2 in or near bract axil in distal portion of axis, not confined to summit, but not becoming scattered along axis; archegonia sometimes only at axis summit, the shoot then appearing acrogynous; in other shoots, the archegonia associated with bracts below the summit, the shoots then fundamentally anacrogynous; bracts associated with archegonia

(unfertilized gynoecia) similar to leaves or smaller. *Perichaetial bracts* associated with fertilized gynoecia erect to suberect at least proximally, some becoming moderately reflexed distally, the bracts longer than wide, somewhat larger than leaves, elliptic (but more narrowly so than leaves) to oblong; accessory bracts (bractlets) often present, in unfertilied gynoecia ca. 0.3 times the leaf size and lingulate, in fertilized gynoecia ca. 0.25–0.5 the size of adjacent bracts and oblong to long-linear, inserted at base of calyptra; archegonial terminal disc not differentiated, no apical dilation of stem with archegonia formation; swollen fertile "nodes" and subsequent apical innovation absent. *Calyptra* single (rarely double) per gynoecium, translucent, long-tubular and with sides ± parallel throughout or elongate-subclavate and gradually expanding distally, the mouth not contracted; calyptra surface smooth, the unfertilized archegonia and accessory bracts remaining at base of calyptra and not elevated upon its surface. Sporophyte not seen.

Ecology-Phytogeography.—The type was collected on a shaded, vertical, clay bank of an intermittent stream at 750 m in a stand of forest made up of *Araucaria muelleri* (emergent species here), *Strasburgeria* (in its own, monotypic family), *Zygogynum* (Winteraceae, all species on New Caledonia), *Sphenostemon, Canacomyrica* (monotypic genus of Myricaceae), *Nemuaron* (Monimiaceae; two species, both from New Caledonia), *Beauprea, Ascarina,* and *Hibbertia.* This species is known only from the type; the genus is new to the flora of New Caledonia.

Branching.—Branching in *H. monoicum* is copious, exogenous intercalary, and consists of a system of erect leafy shoots arising from prostrate, elongated, often intertwined rhizome-like axes. The rhizomes often themselves branch and remain rhizomatous, or they may occasionally gradually convert to erect, leafy axes (Fig. 8). This leafy axis either remains unbranched or gives rise to one or two rhizome-like branches from its extreme base. On very rare occasions (only one branch seen), a leafy, exogenous intercalary branch arises from a leafy axis. In this case the branch issued from the axil of a leaf about midway between the shoot apex and base, and while ascending to the height of the parent axis, was inferior in stature to it. Campbell (1959, p. 249) described such branches, which arise from an epidermal cell and lack a basal sheath, for *H. gibbsiae.* Campbell, however, described branch initiation "on the side of the stem at a point midway between two leaves of a vertical row," and not axillary as in our plant. This branch type in *H. monoicum* is reminiscent of that shown for *H. ovalifolium* by Schuster (1971, fig. 18, right hand branch). There are, then, three possible positions of a leafy shoot, namely 1) directly from a prostrate leafless axis which continues rhizomatous growth; 2) from a rhizome, but through gradual conversion to a leafy shoot; and 3) as an exogenous intercalary branch of another leafy shoot.

The following two branch types found in *H. intermedium* are apparently not produced in our plant: 1) leafless, geotropic stolons originating from above a leaf axil; and 2) terminal, furcate branches (see Schuster, 1967, figs. VI: 1, 6). The branch system of *H. monoicum* is thus rather simplified, at least compared with that of *H. intermedium.* Branching in *H. monoicum* consists of an extensive continuous rhizome system, which at times "acts" like that of *H. gibbsiae.* In that species, "a creeping rhizome becomes ascending and leafy, and near the



FIGURES 1–8. *Haplomitrium monoicum* Engel.—1. Cross section of leaf base.—2–3. Two leaves, and between, a dorsal leaf.—4. Antheridium *in situ*, note stalked and sessile slime papillae (=s).—5. Stalked (left) and sessile slime papillae of androecia.—6. Median leaf cells, with striate-papillose cuticle indicated on some cells.—7. Distal portion of leaf showing border.—8. Habit showing monoecious condition, note antheridia (=♂).

point at which it becomes erect gives rise to a new rhizome-like axis, which again, potentially may become erect" (Schuster, 1967, p. 35).

Attention has been placed on the knobby to spurlike, "coralloid" rhizome of *H. hookeri* which Müller (1909) illustrated and which Schuster (1967) utilized as a key character. However, the rhizome of *H. hookeri* is more variable than these authors would have it. Worley (1969, p. 228), for example, states that his material "is less 'warty' and rather freely extended throughout the substrate . . . ." Further, *Engel 17443* from Mt. Austin, Washington also has elongated nonspurred rhizomes.

Slime Papillae.—Slime papillae of *H. monoicum* occur on stem cells near the shoot apices as well as among antheridia. They may be either sessile or mounted on a cell quite wide in comparison to the slime cell (Figs. 4–5). Sessile slime papillae apparently are exceedingly rare for the family, and, in fact, Schuster (1967, p. 16) states for Calobryaceae, "Slime papillae of a single type: the stalked type." However, sessile slime papillae occur in our plant, as well as on the rhizome of *H. intermedium* (Berrie, 1962). Udar & Chandra (1965b) state that leaf slime papillae in *Haplomitrium* (=*Calobryum*) *indicum* are 1–2(–3) cells high and illustrate a sessile "mucilage papilla" (see their fig. 11).

The leaves of *H. monoicum,* even in their immature state, bear no marginal or surface slime papillae. I was unable to establish leaf slime papillae, at least on progressive stages of leaf development down to the 24- and 32-celled states. In this respect *H. monoicum* is a bit unusual, for the majority of taxa in the genus possess leaf slime papillae (also called mucilage hairs by some authors). Further, the lack of leaf papillae is of taxonomic value, for the allied *H. intermedium* indeed has them (Berrie, 1962).

Leaf Cells.—The leaves have a conspicuous border formed of a single row of cells both larger and thicker-walled than the interior cells (Fig. 7). In surface view, cells of the penultimate row exhibit three thickened walls and a thin innermost fourth wall (Fig. 7). Sporadically and locally there may be a few uniformly thickened cells forming a second row, but this is exceptional (Fig. 7, bottom right). The cells are large for the genus, being 54–70 μm wide and 55–78 μm long in the leaf middle, and thus are comparable in size to those of the non-allied *H. gibbsiae,* which has variable median cells, 40–65 × 40–100 μm, and to *H. andinum,* with median cells 40–70 × 65–105 μm. The cuticle of *H. monoicum* is striolate-papillose (Fig. 6); to my knowledge all other species in the genus have a smooth cuticle.

Sexuality and Gynoecia.—This is the only monoecious species known for order Calobryales (cf. Fig. 8). The archegonia, remarkably, occur in nearly the identical position and number as the antheridia. Archegonia occur only 1–2 per bract, this being the lowest number in the genus. (Also with a reduced number of archegonia is *H. intermedium,* with 4–8 per bract.) In general, the archegonia are not particularly fixed in juxtaposition to the bract, but are rather in, or in the vicinity of, the bract axil or bract base. Some shoots have archegonia solely terminal in position, although their axillary nature is still clearly demonstrable. Such shoots are acrogynous, although there is no apical swelling of the shoot and thus no suggestion of a terminal disc characteristic of subg. *Calobryum.* Other shoots possess archegonia associated with the second and third cycles of leaves

(bracts) below the axis summit. Such shoots are fundamentally anacrogynous. Prior to the work of Schuster (1967), archegonial position was used as a major criterion to separate the acrogynous condition of *Calobryum* and the anacrogynous condition of *Haplomitrium*. Schuster, however, has shown that this character is by no means as absolute as had been thought, and that the two genera in fact merge. Species like *H. intermedium* and now *H. monoicum*, which have both the acrogynous and anacrogynous conditions, are critical to this broader generic concept [which required the combination *Haplomitrium dentatum* (Kumar & Udar) Engel, made above]. Anacrogyny is almost carried to an extreme in *H. intermedium*, where we find distinct swollen archegonia-bearing "nodes" with subsequent and sometimes repeated apical proliferation of the shoot (see Schuster, 1967, fig. IV: 6). Such nodal formation appears to be restricted to that species.

Haplomitrium monoicum, like *H. intermedium*, produces accessory perichaetial bracts (or bractlets). These are inserted at the calyptra base and not elevated upon its surface.

The gynoecia nearly always produce one calyptra per gynoecium, but in rare instances there may be two well-developed calyptrae. The calyptra of *H. monoicum* is smooth throughout and does not have scales or bractlets upon its surface such as we find in, say, *H. gibbsiae*. Unfertilized archegonia remain at the base of the calyptra, and are not elevated upon its surface. This situation is similar to *H. intermedium*, *H. hookeri*, and *H. andinum* in which the calyptra is derived from the venter of the archegonium plus, at most, a limited zone of receptacular tissue beneath the unfertilized archegonia.

Androecia.—Antheridia occur at or near the shoot summit, and are not confined to definite receptacles as in subg. *Calobryum*. In this respect *H. monoicum* compares with *H. hookeri*, *H. ovalifolium* and *H. intermedium*, the last being unique in producing swollen fertile "nodes" with subsequent apical innovations.

The Crosby plant possessed both old, dehisced antheridia as well as ripe and immature, unopened individuals. The dehisced antheridia are interesting, for they are urn-shaped, with the distal half missing but the pale brown basal portion left intact, the overall appearance like that of a dehisced *Physcomitrium* moss capsule.

Schuster (1967, p. 17) states for suborder Calobryinae that "the long stalk of the mature antheridium is notable; longly stalked antheridia being exceptional in the leafy Hepaticae, except for the Schistochilaceae and Perssoniellaceae." The stalk is not only comparatively long, but quite well differentiated from the body of the antheridium; see, for example, the figures of *H. intermedium* in Schuster (1967), of *H. hookeri* in Schuster (1967) and Inoue (1971), of *H. ovalifolium* in Schuster (1971), of *H. andinum* in Fulford (1963), and of *H. blumii* in Goebel (1891, pl. 2; 1930, p. 844) and Campbell (1920).

The antheridia of *H. monoicum*, however, are unique within the family. They are narrowly ovoid to elliptic in shape, with stalks only 1–2 cells high that grade almost imperceptibly into the body of the antheridium, such that the antheridia appear almost sessile (Fig. 4). Antheridia with such abbreviated stalks and minimal differentiation of stalk and body surely must be regarded as the most primitive within the family. Highly abbreviated antheridial stalks, in fact, are rare in hepatics, and the condition in *H. monoicum* brings to mind that of the unrelated

Treubia nana (Metzgeriales), in which the stalks are two cells wide and one cell high (see Inoue, 1960). In that species, however, the stalk cells are very squat and the body is globose.

The question then arises: Is there a connection between the antheridia of our species and the type prevalent in the remainder of species in *Haplomitrium*? The stalk of *H. gibbsiae* appears to be relatively short. According to Campbell (1959), the stalk of the mature antheridium of that species is 3–5 tiers of cells in height. Moreover, the figures of this species in Schuster (1967) are particularly revealing, for the stalks expand somewhat gradually toward the body. Thus, features of the stalk (cell number and stalk form) in *H. gibbsiae* somewhat approach those of *H. monoicum*.

Relationships.—Haplomitrium monoicum belongs to a well-defined ensemble of species that constitutes subgenus *Haplomitrium*. These taxa are *H. monoicum*, *H. intermedium*, *H. ovalifolium*[3], and *H. hookeri*, and are characterized by 1) archegonia and antheridia at least in part scattered and indefinite in position and not consistently confined to terminal receptacles, the archegonial shoots at least in some cases thus anacrogynous; 2) shoots at least potentially indeterminate in growth and leafy throughout their length, bearing a number of cycles of mature leaves; 3) leaves of sterile shoots subequal in size throughout axis, usually longer than wide and either unistratose throughout or with a limited field of polystraty at extreme base; and 4) antheridia yellow to pale orange (except *H. monoicum*).

The nearest, but not particularly close, relative of *H. monoicum* is *H. intermedium* of Australia. The two taxa share such features as 1) large leaf cells, being 54–70 μm wide and 55–80 μm long; 2) general elliptic leaf shape, although *H. intermedium* varies toward an ovate outline; 3) accessory perichaetial bracts or bractlets; and 4) small plant size.

Haplomitrium monoicum is noticeably distinct from *H. intermedium*, differing from that species in 1) the bordered leaves; 2) the completely entire leaves, which do not develop slime papillae, even on very young leaves; 3) the broadly rounded leaf apices; 4) the bistratose leaf base; 5) the striolate-papillose leaf cuticle; 6) the nonpigmented antheridia with stalks only 1–2 cells high, and with stalk and body gradually merging; 7) the lack of stolons and terminal branches; 8) the reduced number of archegonia per bract; and 9) the monoecious condition. The magnitude of these differences, together with the number of unspecialized features—namely 2), 6), 7) and 8) above—speak for a very unspecialized species which belongs in a section of its own, as follows:

Haplomitrium sect. **Protohaplomitrium** Engel, sect. nov.

Planta monoica, rhizomatibus basalibus et erectis axibus foliosis solum instructa; stolones et rami terminales nulli. Cellulae marginales foliorum uniseriatae, medianis grandiora et parietibus crassioribus; cuticula foliorum striolato-papillosa; papillae mucigerae foliorum maturarum atque immaturarum nullae. Antheridia archegoniaque ad apicem axis vel prope hunc posita, 1–2 per bracteam, non in

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[3] Since *H. ovalifolium* is known with sparing gynoecial plants, the anacrogyny of this species has not been firmly established. However, Schuster (1971, p. 139) states that "isolated archegonia occasionally [are] present in the axils of subfloral bracts." Further, the vegetative plants and scattered antheridia closely match those in subg. *Haplomitrium*, and I do not hesitate to place it there.

distinctum receptaculo termini aggregata. Antheridia matura eburnea, anguste ovoidea vel ellipsoidea; pedicellus 1–2 cellulae longus, crassus, a corpore antheridii vix distinctus.

TYPE: *Haplomitrium monoicum* Engel.

With the discovery of *H. monoicum* and *H. ovalifolium* (Schuster, 1971), there has been a reduction in degree of isolation of the monotypic subgenus *Archibryum* that Schuster (1967) had established for *H. intermedium*. I would prefer a sectional level for that species, as follows:

Haplomitrium sect. *Archibryum* (Schust.) Engel, stat. nov. Basionym: *Haplomitrium* subg. *Archibryum* Schust. Nova Hedwigia 13:28. 1967.

The taxa of subgenus *Haplomitrium* may be separated by the following key:

KEY TO TAXA OF *HAPLOMITRIUM* SUBG. *HAPLOMITRIUM*

1a. Leaves with a conspicuous border of large thick-walled cells, the interior cells smaller and leptodermous; leaf apices mostly broadly rounded; leaf margins completely entire, not repand, without tendency toward lateral teeth or lobes; leaf slime papillae lacking, even on young leaves; cuticle striolate-papillose; antheridia ivory white, the stalks 1–2 cells high, gradually and almost imperceptibly grading into body; plants monoecious. New Caledonia. Sect. *Protohaplomitrium* .... *H. monoicum*

1b. Leaves without a border; leaf apices variable, ranging from narrowly rounded to blunt to blunt pointed; leaf margins often repand to repand-lobate, sometimes with teeth or lobes; leaf slime papillae present, at least on young leaves (? *H. ovalifolium*); cuticle smooth; antheridia yellow to light orange, the stalk and body clearly differentiated and not gradually merging, subequal in length; plants dioecious .... 2.

2a. Leaf cells large, 40–50 μm wide, 55–80 μm long; branching complex: besides upright leafy shoots and basal rhizomatous axes the plants developing 1) leafless, geotropic stolons originating from above a leaf axil, and 2) terminal furcate branches; androecial shoots with conspicuous, swollen fertile "nodes" with subsequent, sometimes repeated, apical proliferation of the shoot; leaves unistratose throughout. Australia. Sect. *Archibryum* .... *H. intermedium*

2b. Leaf cells small, 24–45 μm wide, 25–55 μm long; branching simple: besides upright leafy axes and basal rhizomatous axes, the plants developing only exogenous intercalary branches of leafy shoots, the plants without stolons or terminal branches; androecial shoots of ± the same width throughout, without swollen "nodes"; leaves with a small, basal, at least bistratose field, the leaves otherwise unistratose. Sect. *Haplomitrium* .... 3.

3a. Leaves never bifid, often diamond shaped to ovate-triangular, mostly with a low terminal lobe and 2 obtuse lateral lobes, the leaves sometimes wider than long; oil-bodies usually homogenous. Northern Hemisphere .... *H. hookeri*

3b. Leaves sometimes bifid to base, mostly ovate to ovate-lanceolate, the margins at most obscurely repand to repand dentate, not lobed, the leaves always longer than broad; oil-bodies ± clearly botryoidal. New Zealand, Campbell Island .... *H. ovalifolium*

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NOTES

TWO NEW SPECIES OF *BONAFOUSIA* (APOCYNACEAE) FROM PANAMA AND COLOMBIA-ECUADOR

Bonafousia panamensis Markgraf, Boiteau & Allorge. TYPE: *Gentry 6847* (Z, holotype; MO, isotype).—FIG. 1.

Arbuscula ad 7 m alta. Ramiculi crassiusculi, angulosi. Folia decussata, petiolus crassus, 1–1.5 cm longus, basi intus collo intropetiolari 3 mm alto instructus; lamina membranacea, maxima, usque ad 50 cm longa et 18 cm lata, elliptica, apice breviter acuminata, basi longe angustata, glabra, in sicco lutescens, subtus minute papillosa et glandulis sparsis punctata; nervi laterales arcuati, ad 3 cm inter se distentes, 18–20 in utroque latere. *Inflorescentia* axillaris, glabra, cymosa, 6 cm alta et lata; pedunculus crassus, 0.5–1 cm longus; bracteae ovatae, obtusae, 2–3 mm longae, 1 mm latae; pedicelli 4–6 mm longi. Lobi calycis oblongo-ovati, obtusi, membranacei, inaequales, 1–1.4 cm longi, 0.8 mm lati, intus multiglandulosi. *Corolla* dilute lutea, glabra, hypocraterimorpha; tubus albus, 12–20 mm longus, 4 mm latus, infra faucem dextrorsum tortus; alabastrum loborum luteum, globosum, tubo aequilatum; lobi explanati 5 mm alti, dolabriformes, lateraliter ad 8–9 mm elongati, obtusi. Antherae infra faucem insertae, sagittatae, 4–6.5 mm longae, 1 mm latae, caudis basalibus leviter incurvatis. Caput stigmatis antheris arcte appressum, supra globosum et 5-gibbum, infra umbraculiforme. Ovarium apocarpum, biloculare, glabrum, conicum, 1.5 mm altum et latum, disco 1 mm alto, anuliformi insidens. *Mericarpium* oblique globosum, calice persistente. Semina ovoidea, 1 cm longa, arillo rimoso induta. Embryo rectus, cotyledones ovato-oblongi, 2 mm longi, radicula, 2.5 mm longa.

Specimens examined: PANAMA: Province Bocas del Toro: Region of Almirante, Buena Vista Camp on Chiriqui trail, 1250 ft. 1–3. 1928. *Cooper 610,* NY; Province Cocle: Vicinity of La Mesa, N of El Valle, 1000 m, *Allen 2804*; hills of El Valle, *Allen 2953,* GH; N slope and summit of Cerro Pilon, 900–1173 m, *Croat 14319, Croat 22919,* GH, NY; Slopes of Cerro Pilon, *Duke 12173, 13161, 14651*; La Mesa, El Valle, Cerro Pilon, *Dwyer 3574a, 8299, 8362, 11900,* GH; Cerro Pilon, 2700 m, *Dwyer 8688*; Cerro Gaital Caracoral, *Dwyer & Correa 8862, 8912*; Summit of Cerro Pilon, *Dwyer et al. 4502b*; Cerro Pilon, base, *Gentry & Dwyer 3645*; El Valle, Cerro Pilon, *Kirkbride 1047, 1080*; Cerro Pilon, *Lallathin 27-4,* NY; Cerro Pilon, *Liesner 784,* GH; Province Colon: Sta Rita Ridge, 4–5 miles Transisthmian hwy, 500–800 m, *Gentry 6100,* Z; Sta Rita Ridge, Boyd Roosevelt hwy, *Mori & Crosby 6420*; Province Darien: Vicinity Cerro Tacarcuna, *Gentry & Mori 14054*; Province Panama: Road to Carti, 15 km of El Llano, *Busey 372*; El Indio, Rio Cascada, region Cerro Jefe, 750 m, *Correa & Dressler 1777*; Cerro Camapan, 800 m, *Croat 22809*; 1000 m, *Croat 22809,* NY; El Llano-Carti Road, *Croat 25168*; El Llano-Carti Road, *Dressler 4281*; Cerro Jefe, 3100 ft, *Dwyer & Gentry 9519*; Cerro Camapan, *Gentry 1855, 4951, 5784,* Z; El Llano-Carti, *Kennedy 2686*; Altos de Rio Pacora, 2500 ft., *Lewis, MacBride et al. 2297*; Cerro Camapan, 850 m, *Liesner 632*; La Eneida, 1000 m, *Luteyn & Foster 1125,* NY; Cerro Camapan, El Llano-Carti and Altos de Pacora, *Mori & Kallunki 3571, 4553, 6047*; El Llano-

ANN. MISSOURI BOT. GARD. 68: 677–686. 1981.

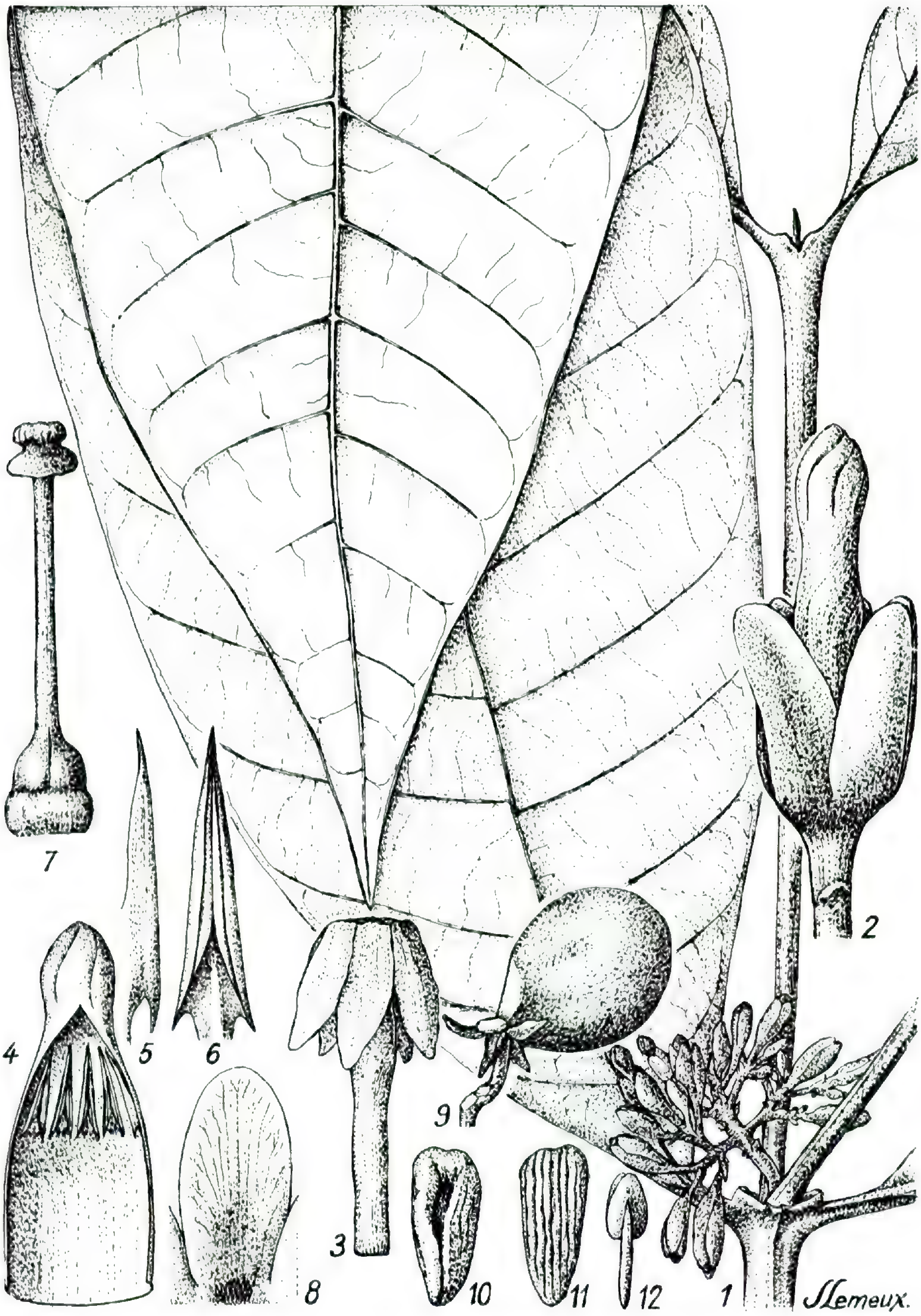

FIGURE 1. *Bonafousia panamensis* Markgraf, Boifeau, & Allorge: 1.—flowering twig ×⅔; 2.—flower bud ×⅔; *Gentry 6847*. 3.—corolla ×2; *Croat 22919*. 4.—corolla of flower bud cut longitudinally below and laid flat ×2; 5.—stamen, front view ×6; 6.—stamen, side view ×6; 7.—gynoecium with its clavuncle ×4; 8.—sepal with glands, inner view ×2; *Gentry 6847*. 9.—fruit, a mericarp removed ×⅔; *Gentry 6100*. 10.—seed, inner side ×2; 11.—seed, outer side ×2; 12.—embryo ×2; *Gentry & Dwyer 3645*.

Carti, *Nee & Warmbrodt 10377*; Province San Blas: San Blas-Darien Road, Rio Membrilla, *Duke 10876*; Vicinity of Puerto Obaldia, *Mori 6869*; Plain of Sperdi, near Puerto Obaldia, *Pittier 4354*; Province Veraguas: Between Alto Piedra School and Rio Colovebora, *Croat & Folsom 34103*; NW of Santa Fe, *Mori & Kallunki 5348*; 7 km W of Santa Fe, *Nee 11159*.

The first quoted material for this species was mentioned by Woodson & Shery (1942) under the name of *Bonafousia sananho* (R & P) Mgf. Nowicke (1970) used this same name in the Flora of Panama. This species is, however, easily distinguished from *Bonafousia sananho* because it has a much larger calyx with many glands at the base, with lobes not equal to half the tube, etc. The major part of the material examined was from MO; the other herbaria are specified.

Bonafousia columbiensis Allorge. TYPE: Colombia: Espriella, Tumaco, 20 June 1959, *Castañeda 2799* (MO, holotype).—FIG. 2.

Frutex vel arbuscula 3–10 m alta; cortice cinero-fusco, rimoso; latice albo. Ramiculi tenui, cylindracei, absque canalibus, dichotomi. Folia opposita, lanceolata, 11–20 cm longa, 3–5 cm lata, longe acuminata, acumine 1–2 cm longo, membranaceae, sicca luteola, petiolo 0.5–1 cm longo, nervis utraque pagina manifestis, 0.5–1 cm distantibus. *Inflorescentiae* pauciflorae, saepe recurvatae, pedunculo subnullo, pedicellis 0.3–0.5 cm longis, bracteis triangularibus 1 mm longis. Flos albus fauce lutea vel crocea. Calyx dentibus obtusis, glaber viridis, margine ciliatus, basi interne 3–5 glandibus instructus; *Corollae* tubo 1–5 cm longo, glabro extra interneque basi, indumento infrastaminalis zonis infrastaminalibus filamentis paribus disposito. Lobi corollini initio contorti, dein reflexi, medium tubi haud superantes. Alabastrum sphaerocephalum obtusum. Discus distinctus ex ovario erigens, ad dimidium calycis tubi attingens. Carpella longe in stylum descrescentia; clavuncula basali coronula continua et appendicibus brevissimis a latere invisibilibus munita. *Fructus* luteus, mericarpiis duobus recurvatis, acuminatis, granulosis, compositus, 4 × 2 × 2.5 cm metientibus. Pulpa alba, dulcis, edulis; semina fusca longitrorsum sulcata. Embryo radicula recta, longiore quam cotyledonibus (2.5 mm vice 2 mm longa) cotyledonibus cordatis. A *B. chocoensis* Gentry differet foliis petiolatis, inflorescentia pauciflora, fructuque minus globosa, non laeve. A *B. sananho* (R & P) Mgf. et *B. tetrastachya* (HBK) Mgf. quibus saepe confusa est, differet i.a. lobis corollinis medium tubi haud superantibus.

Specimens examined: COLOMBIA: La Guayacana, Tumaco, *Castañeda 2920*. ECUADOR: Province Pichincha, 20 km W of Sto Domingo de los Colorados, 1000 m, *Cazalet & Pennington 5166*, K, NY; Province Los Rios, Rio Palenque, 150–220 m, *Dodson 5457, Dodson 6611; Dodson & McMahon 5025*, NY; Province Oriente, Napo Pastaza and Bobonaza, 1000 m, *Gill 14*, NY; Province Pichincha, Rio Toachi near Sto Domingo, 700 m, *Jativa 527*, NY; 37 km S of Sto Domingo, *Pennington 86 SD*, K, NY; foot of Western Cordillera, *Rimbach 45*, GH; mentioned as a sp. nov. of Peru, but at that time Peru included Ecuador, *Ruiz & Pavon s.n.*; Mt. Chimborazo, 2500 m, *Spruce s.n.*, K.

The illustrations published by Romero Castañeda (1961) must refer to this species rather than to *Bonafousia tetrastachya* as he indicated, since the lobes

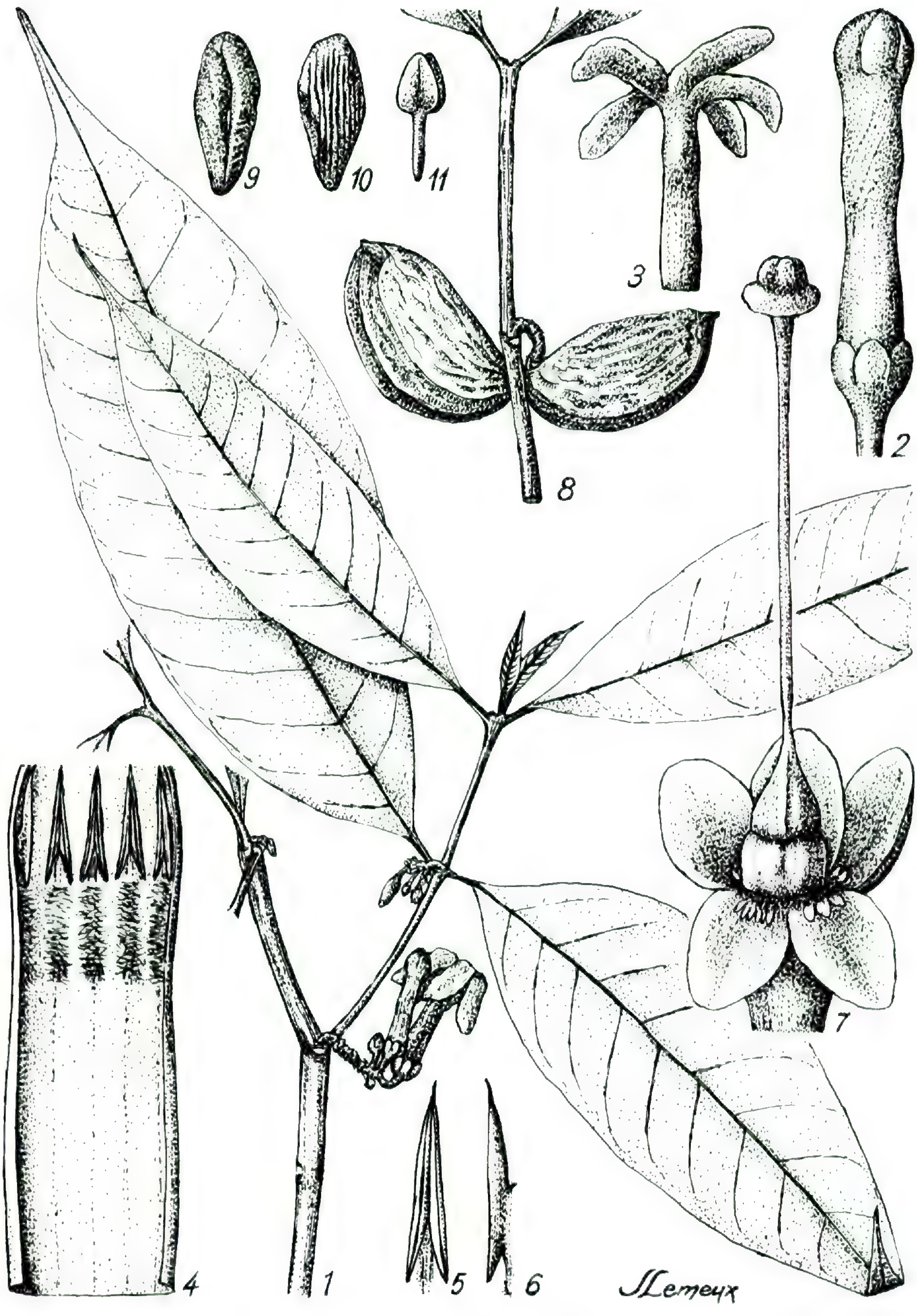

FIGURE 2. *Bonafousia columbiensis* Allorge: 1.—flowering twigs ×⅔; *Ruiz et Pavon*, G, Herb. Boissier; 2.—flower bud ×2; *Dodson 5457*. 3.—corolla ×2; *Cazalet et al. 5166*. 4.—corolla of flower bud cut longitudinally below and laid flat ×4; 5.—stamen, front view ×6; 6.—stamen, side view ×6; 7.—gynoecium with its clavuncle ×6; *Dodson 5457*. 8.—fruit ×⅔; *Dodson 6611*. 9.—seed, ventral side ×2; 10.—seed, dorsal side ×2; 11.—embryo ×2; *Dodson et MacMahon 5025*.

are shorter than half of the tube of the corolla. According to the map of vegetation types of Ecuador published by G. Harling (1979), the distribution of this species is found in the "lowland and lower montane rain forest" zones at an altitude of 100–2500 m.

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—F. Markgraf, Botanischer Garten, Zollikerstrasse 107, CH-8008, Zurich, Switzerland, P. Boiteau, and L. Allorge, Laboratoire de Phanérogamie, Museum National d'Histoire Naturelle, 16 Rue Buffon, 75005, Paris.

STUDIES IN THE CAPPARIDACEAE XV: *CAPPARIS PANAMENSIS*, N. SP.[1]

Capparis panamensis Iltis, **sp. nov.** TYPE: Panama, Prov. of Panamá, El Llano-Cartí Road, 12 km from Inter-American highway, wet forest 350 m alt. 15 Feb. 1975 (fl). *Mori, Kallunki & A. Gentry 4632* (WIS, holotype; MO, US, isotypes).—FIG. 1–2.

Arbores parvae, stellato-pubescentes; similis *Capparis pittieri*, sed foliis oblongo-ellipticis coriaceis perennibusque, subtus flavovirentibus, inflorescentibus laxioribus grandioribusque, et floribus grandioribus; sylvae tropicae Panamae endemica.

Small *trees* 5–6 m tall. *Branches* with ± protruding leaf scar bases, the youngest, leaf-bearing ones rusty-brown stellate-pubescent, 2–3 mm in diameter, becoming in the second year dark red-brown and verrucose and 3–6 mm or more in diameter.

Leaves alternate, spaced 1–3 cm apart, 4–7 on each branchlet, *oblong-elliptic* (rarely slightly oblanceolate-elliptic), broadly acute to abruptly acuminate and/or rounded at apex, broadly cuneate to rounded at base, (5–)8–17 cm long, (2–)4–6(–8) cm broad, stellate-pubescent on both sides when young, becoming glabrous and somewhat varnished, evergreen and *stiffly coriaceous*, with quite entire and slightly revolute margins, in herbarium material *dark green above, markedly yellow-green beneath*; main lateral nerves 5–8, the midrib and lateral nerve network prominent on both sides, but the smaller veins buried in the thick blade tissue. *Petioles 8–15(–24) mm long*.

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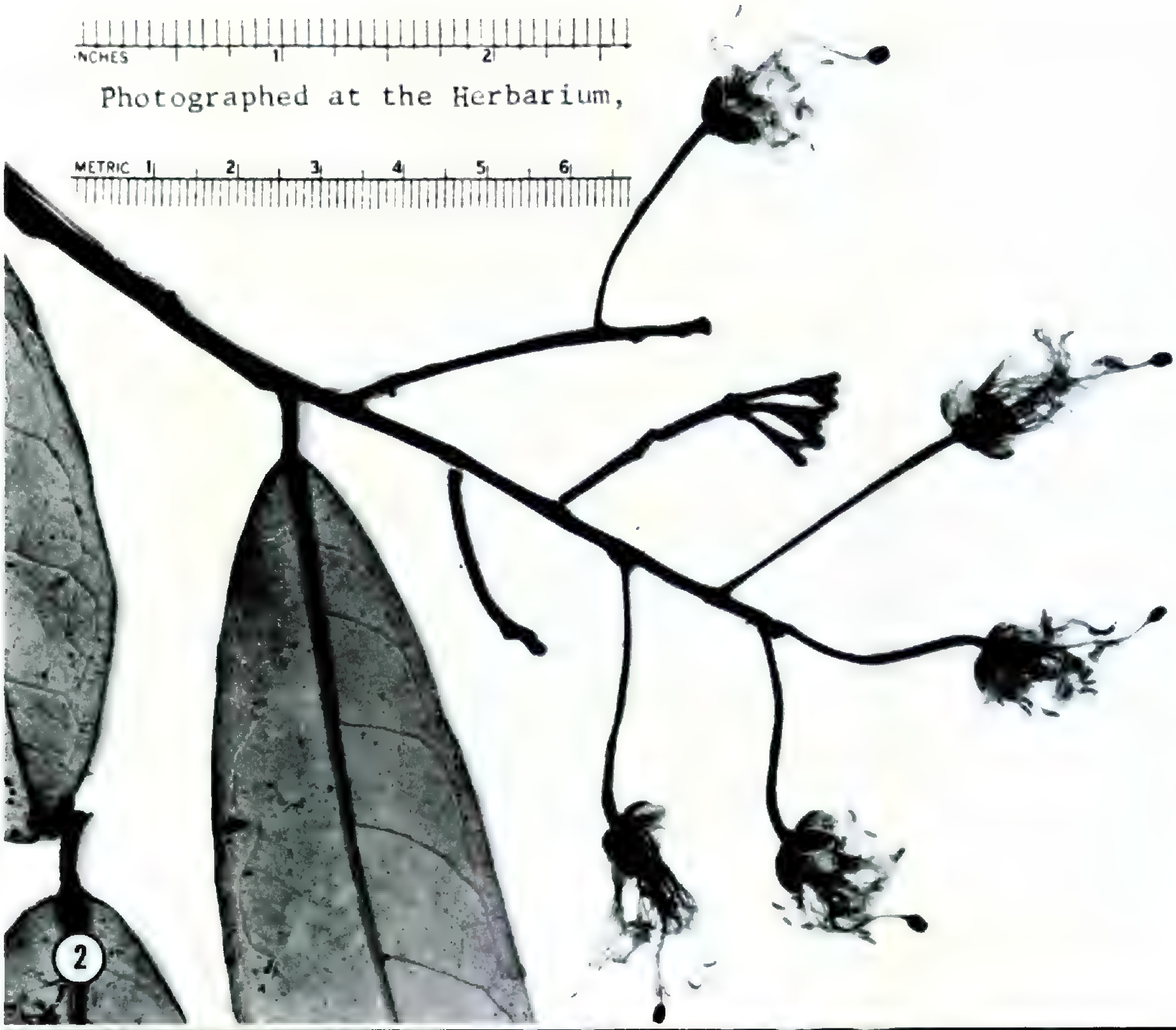
[1] I thank Alwyn Gentry for his photograph, and Duane Kolterman for the drawing of the distribution map.

FIGURE 1. Holotype of *Capparis panamensis* Iltis, *Mori, Kallunki & Gentry 4632* (WIS).

Inflorescences compound, terminal on lateral leafy branches, with up to 3–11 flowers in bloom at one time, these long-pedicellate, hence the inflorescences *very open,* 8–20 cm wide and long, *densely rusty-stellate* throughout, bracteate, but bracts minute (1–1.2 mm long, oblong, densely rusty-stellate) and caducous, *the blooming of the 1–8 racemes staggered,* the terminal (central) raceme [with a mature central axis (5–)7–14 cm long] blooming first, the lateral (then still in very young bud and only 2–4 cm long) ending in 1–3 tightly clustered corymbiform racemes with many crowded small (1–2 mm) buds, their axes at anthesis eventually elongating (to 6 cm). Pedicels in young inflorescences very short (2–3 mm),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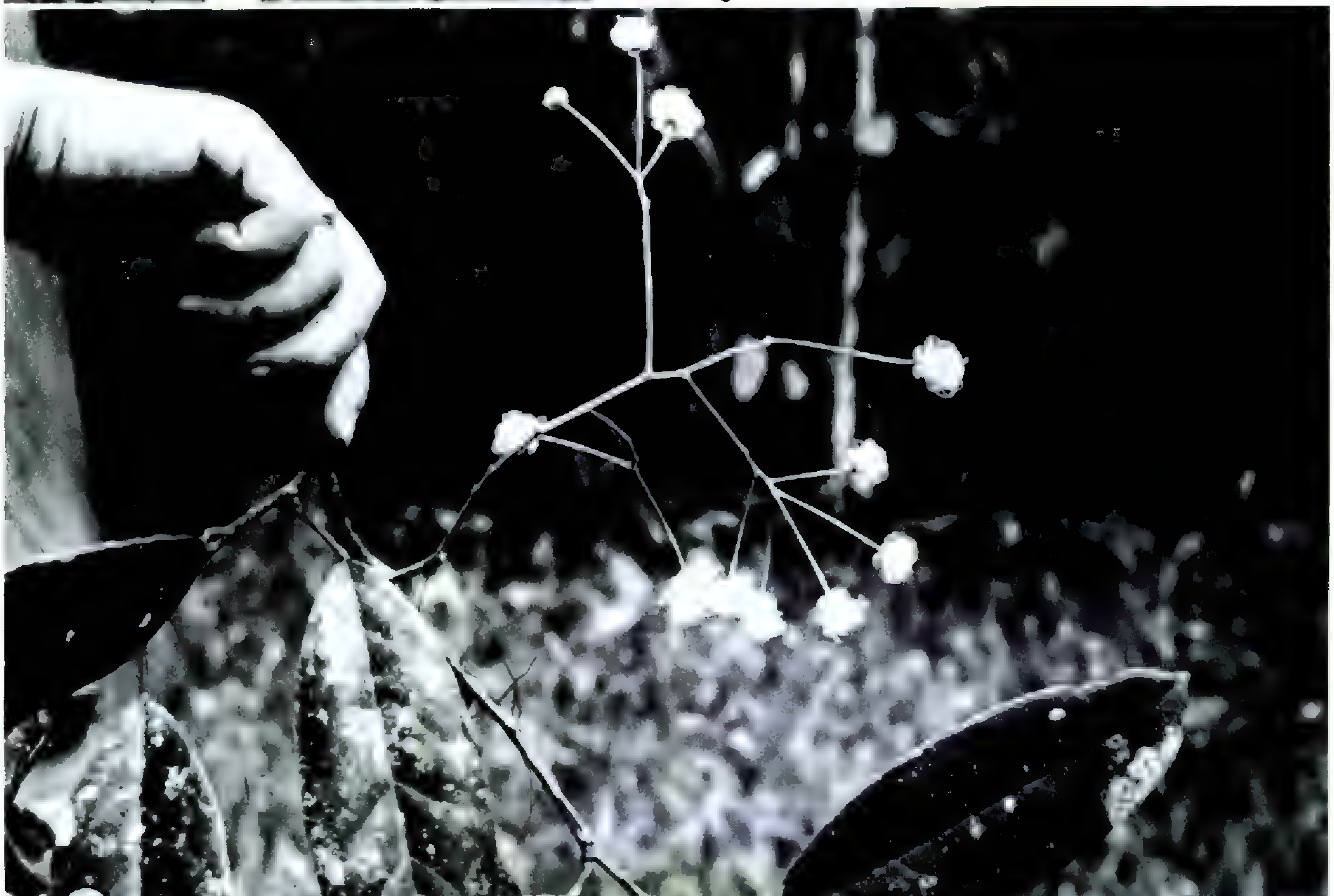
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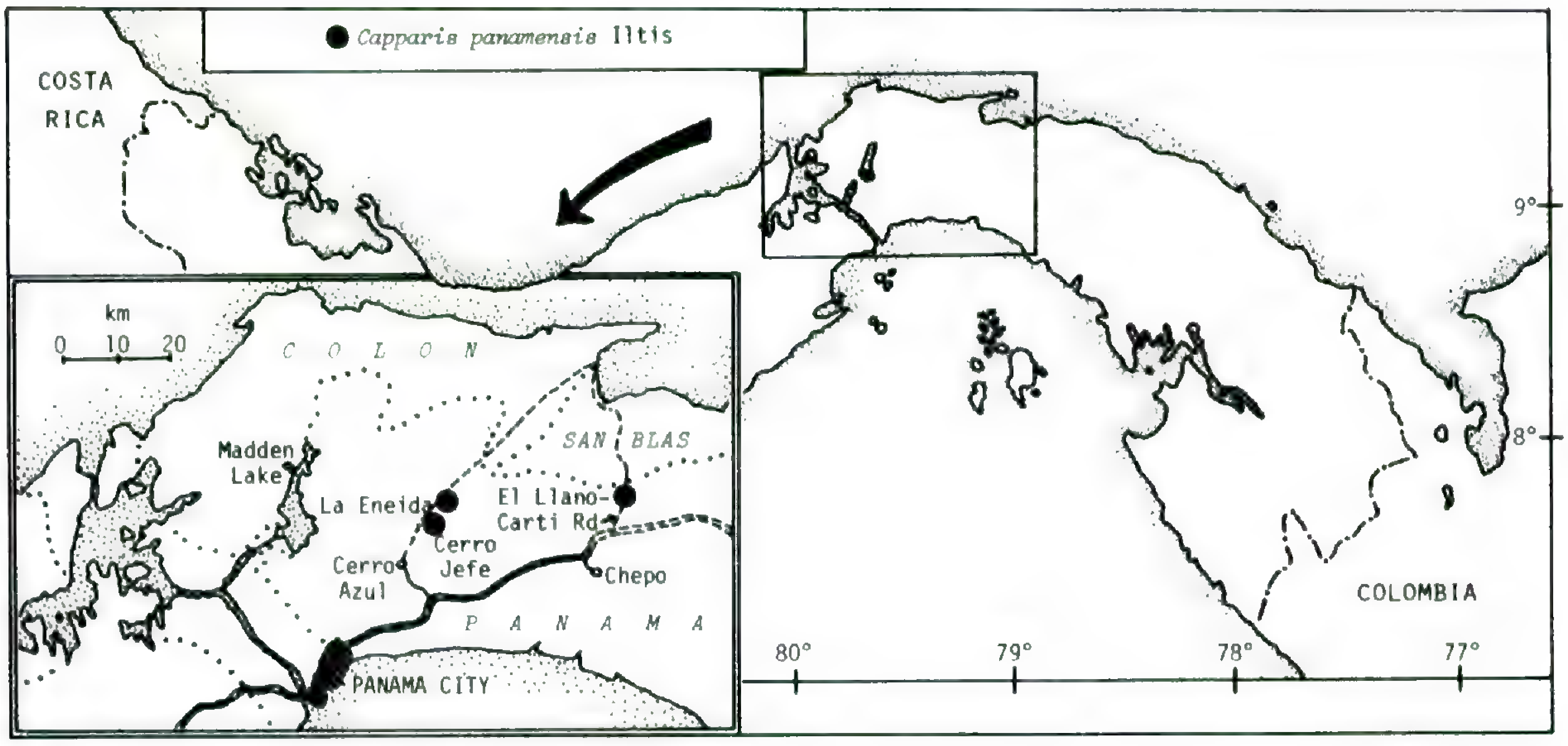

FIGURE 4. Geographic distribution of *Capparis panamensis* Iltis.

greatly elongating when approaching flowering, at anthesis 25–35 mm or more long, very slender; mature buds 5 mm in diameter, with closed aestivation (sepals completely enclosing petals and these in turn the stamens).

Flowers actinomorphic, the sepals horizontal-divergent, the petals slightly ascending. *Sepals imbricate,* in two series, the ab- and adaxial ones on the outside and densely rusty pubescent throughout, the lateral pair on the inside and rusty-stellate only on the exposed central band and pale greenish-white-stellate on the overlapped margins, *broadly ovate-cucullate, ascending, acute, 6 mm long, 3.5 mm broad*; hairs stellate, the *center of each stellate complex rusty-red brown,* the ray hairs relatively thick and pale. *Petals yellow-green,* broadly elliptic, acute to broadly acuminate, 6–7 mm long, 3 mm wide, *densely stellate pubescent without, the hairs yellowish-white* throughout, with ray hairs very slender; both sepals and petals glabrous within. *Nectariferous scales* 4, fleshy, borne between and outside of the petal bases in the axils of the sepals, 1.5 mm wide, less than 1 mm high. *Stamens 28–34* (or fewer?), *20–23 mm long, glabrous, tending to curl* into the flower after anthesis (or during the day?; see Fig. 2), borne on a 1.5–2 mm long androgynophore; anthers 2 mm long. *Gynophore 18–23 mm long,* elongating in older flowers to 45 mm; ovary urceolate-truncate, 2–3 mm long, 1.5 mm in diameter, the sessile stigma broadly truncate-concave. *Fruits* unknown, but judging from flowering ovaries evidently spherical or ovoid; young fruiting pedicel 52 mm long; gynophore at least 50 mm long (in *Dressler 4317*).

Distribution: Endemic to Panama, on ridges east of the Panama Canal, at elevations of 350 m, in wet tropical forests.

Additional collections: Panama: Prov. of Panamá: La Eneida, ca. 16 km east of Cerro Azul (Goofy Lake). 5 April 1973, *R. L. Dressler 4317* (MO, photos WIS); Cerro Jefe, *A. Gentry, J. Dwyer & E. Tyson 3495* [photo in WIS from Kodachrome taken by Gentry—our Fig. 2—this specimen not available, perhaps lost in a fire (see below)]. (These two stations are very close to each other.)

←

FIGURE 2. Holotype of *Capparis panamensis* Iltis. Close-up of inflorescence.

FIGURE 3. *Capparis panamensis* Iltis. Photograph of *Gentry, Dwyer & Tyson 3495,* from La Eneida, Panama. (Photo, Gentry, from Kodachrome slide.)

This distinctive stellate-pubescent, round-fruited species is closely related to *C. pittieri* Standl., from which it differs by much larger and much more open inflorescences, larger flowers (15 mm vs. 10 mm diameter), shorter (20–23 vs 23–32 mm) but more abundant stamens (28–32 vs 16), and much thicker, leathery, more oblong, more abruptly acuminate or rounded leaves that are characteristically yellow-green beneath. The four nectariferous scales are much like those of *C. pittieri* in size and shape.

This species was first brought to my attention through one of Alwyn Gentry's excellent Kodachrome slides, which I was unable to identify to species, especially since the specimens of that collection were all lost when that expedition's presses caught on fire. Soon, however, Dr. R. L. Dressler sent a specimen that matched the picture; and two years later, the three collectors of the type, all former students of mine, collected material which beautifully matched the photograph of the lost original collection.

It is truly remarkable that still another endemic *Capparis* has appeared from the Isthmus of Panama, in addition to the incredible *C. mirifica* Standl. and the ecologically remarkable "detritophilous" *C. antonensis* Woods., which, like *C. panamensis* and *C. pittieri,* grow near the El Llano-Cartí road, northeast and east-northeast of Panama City and close to the Panama Canal, one of the supposedly best collected areas of the Neotropics.

Like so many others, the species is exceedingly rare and evidently threatened with extinction.

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ON THE TRUE IDENTITY OF *LAGENANTHUS PARVIFLORUS* EWAN (GENTIANACEAE)

During the last three years a team of several students and myself has been engaged in a revision of the genus *Lisianthius* s.l. (*Adenolisianthus, Calolisianthus, Chelonanthus, Helia, Irlbachia, Lagenanthus, Lehmanniella, Pagaea, Purdieanthus,* and *Symbolanthus*). Dr. R. E. Weaver (Arnold Arboretum) is involved in revisional work of the two remaining genera *Lisianthius* s.s. and *Macrocarpaea.*

Recently we started studying *Lagenanthus,* a genus that had previously been revised by J. Ewan (1948). Ewan distinguished in his publication two species in this genus: 1. *Lagenanthus princeps,* a very spectacular species with 12–14 cm long, slightly inflated flowers. It is restricted to montane forests in Colombia and W. Venezuela, at elevations of 2500–3000 m. 2. *Lagenanthus parviflorus,* a species that occurs in Panama (hills N of El Valle de Antón, prov. Coclé, alt. 1000 m). In the original description Ewan remarked: "The discovery of this second species of *Lagenanthus* is of phytogeographic interest for it points to an

important floristic relationship prevailing between Panamá and the Colombian-Venezuelan borderlands . . . ." Some of the characteristics of *L. parviflorus* are: lepidote-puberulent branches, corky-thickened bark, calyx-lobes filiform-subulate, leaves very finely granulose-roughened. Since none of these characters normally occur in neotropical Gentianaceae, I became highly suspicious about the real identity of *L. parviflorus*, and a study of the type specimen in MO (*P. H. Allen 3601*, 20 July 1946) confirmed my doubts: *L. parviflorus* does not belong in Gentianaceae. The calyx and enclosed ovary are missing from the holotype sheet; they are preserved in spirit separately, and I did not have the pickled parts at my disposal. With some important information thus not available to me, I at first had difficulty in trying to identify the type of *L. parviflorus* to its true taxonomic place. Fortunately I then remembered an epiphytic Rubiaceae that I had collected in Costa Rica in 1974 and that was determined as *Ravnia triflora* Oersted. Comparison of this collection (*Maas 1487*) with the holotype of *L. parviflorus* and consultation of Dwyer's (1980) description of *Ravnia triflora* in Flora of Panama brought me to the conclusion: *Lagenanthus parviflorus* in reality is *Ravnia triflora* Oersted, and thus belongs in Rubiaceae! The monotypic genus *Ravnia* is restricted to Panama and Costa Rica, and Allen's collection from El Valle de Antón completely fits in that pattern. Ewan's remark on the distribution of *Lagenanthus* should be discarded.

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A brief Latin diagnosis for each new taxon is preferred to a complete Latin description. A complete description should be given in English.

Use one paragraph per basionym as follows: taxon, author, literature citation, type citation e.g., *Dietes flavida* Obermeyer, Fl. Pl. Africa 149: *tab. 1488.* 1967. Type: South Africa, Natal, Jozini Dam, *Admiraal 5293* (PRE, holotype). Descriptions should follow style found in other Annals issues, e.g., in Goldblatt, 1981 (68:132–153). Keys should be dichotomous, indented, with numbered couplets. Cite representative specimens as follows: Mexico, Oaxaca: Sierra San Pedro Nolesco, Talea, *Jurgensen 865* (BM, G, K, US). Use herbarium acronyms as listed in Index Herbariorum (Reg. Veg. 106).

Abbreviations should be checked for consistency and to make sure they are unambiguous. Periods are used after all abbreviations except measures, compass directions, and herbarium designations. Send copies of illustrations; originals will be requested after the manuscript is accepted. All illustrative materials should be mounted on stiff cardboard. A maximum size of a printed illustration is 5″ × 7″, and therefore the height of an illustration must not exceed 1.5 its width. Figures are numbered consecutively with Arabic numerals. Photographs should be sharp, glossy prints. Abut edges of photographs in composite plates. Do not mix line copy and continuous tone illustrations on one plate. Maps should include a metric scale and reference to latitude and longitude; where appropriate, size and scale should be included in photograph or drawings, not in figure legends. Explain all scales and symbols in figures themselves, not in legends. Authors wishing to have original illustrations returned must notify the editor when proofs are returned.

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